THE BREEDING BIOLOGY AND BEHAVIOUR OF THE YELLOW-BREASTED TIT (*PETROICA MACROCEPHALA MACROCEPHALA*)

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by

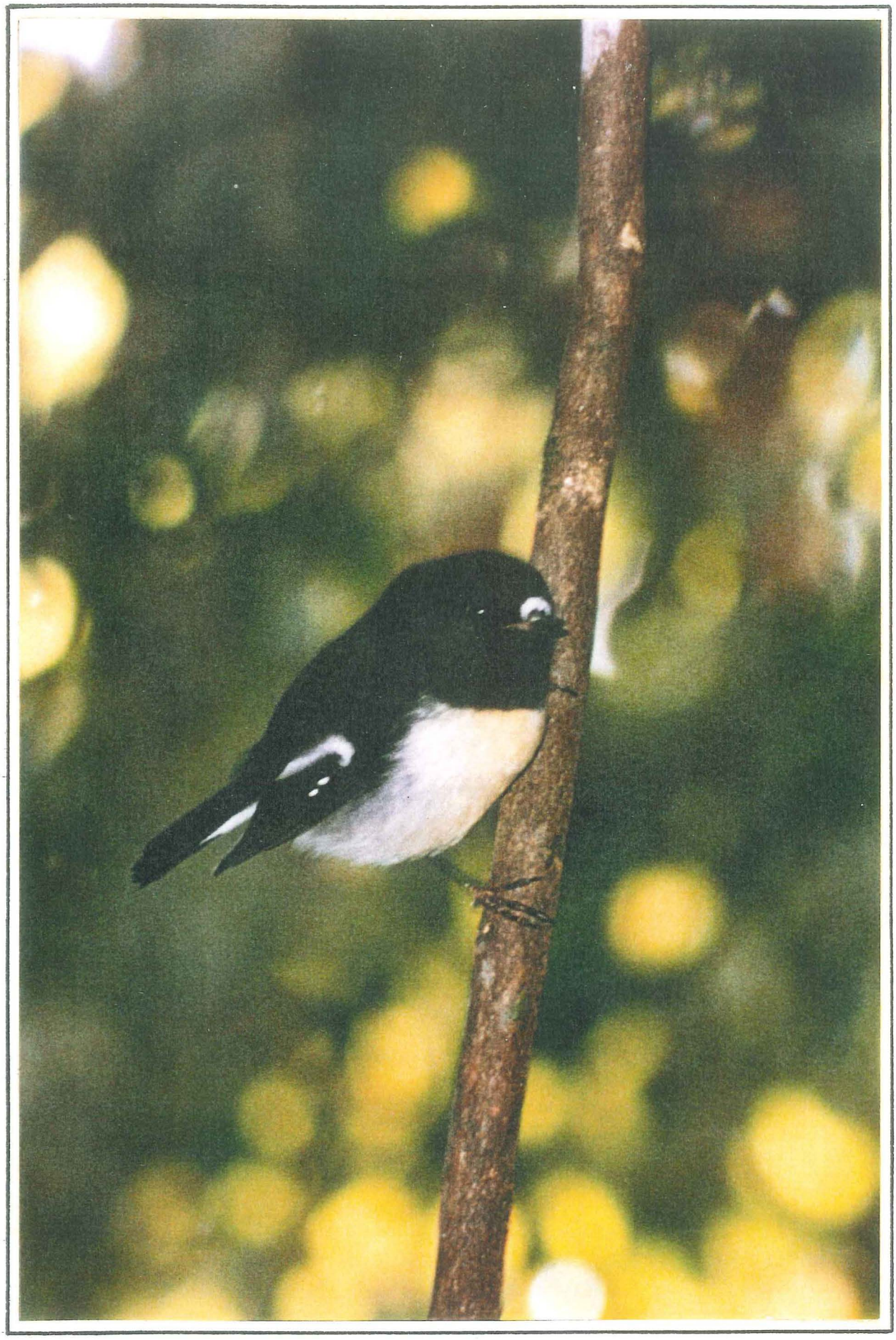
Paul M. Kearton

University of Canterbury

October, 1979.

Frontispiece:

A male Yellow-breasted tit
in faded plumage at the
end of the breeding season.



"Although the New-Zealand avifauna is
the most perfectly known division of our
zoological province, new facts in the
life-history of some of the species are
occasionally presented to the ornithologist....
In the individual history of most species
Buller has left little of interest to be added;
in others additional features in their habits
will transpire as colonization spreads and the
country becomes more settled."

W.W. Smith, 1893.

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ABSTRACT

The breeding biology, territorial behaviour, movements of banded birds, nest sites and nests, feeding biology and vocalizations of a population of Yellow-breasted tits (*Petroica macrocephala macrocephala*) were studied in Mount Fitzgerald Scenic Reserve, Banks Peninsula, during 1977-1979.

Pairs of Yellow-breasted tits remained on a territory throughout the year. Territorial advertisement and defence were at a peak during the late prebreeding season and breeding season. Boundaries were maintained through vocalizations, body-feather and wing displays, chases and, more rarely, fights.

The territorial nature of, and the intolerance towards, other tits were seen developing while fledglings were still being fed by their parents. Shortly after independence, some juvenile males and females set up small subterritories on the peripheries of adult territories. A synchronous movement by some juveniles away from adult territories occurred five to six weeks after independence.

Breeding activities commenced in early September in all pairs and continued to late February for some pairs. The cupular nests were built in four site-types in my study area. A maximum of three broods per pair was raised to independence per season, but one or two was more usual. Brood size varied between three and five. The female renested within two to three days of the previous brood fledging, while the male continued to feed the fledglings. Circumstantial evidence suggested that up to six eggs per clutch could be laid. The behaviour of tits of all ages throughout the breeding season is described.

A wide range of invertebrate prey was taken. Berries may also have been eaten. Prey were captured using the "watch and wait"

technique. No active foraging was observed. Four methods were employed to capture the prey.

The song of the adult male was the most distinctive vocalization of a wide range of calls given by Yellow-breasted tits of all ages. Sonagrams were produced to show and compare the structures of different calls. The developmental stages of male song are also described. Neighbouring males tended to have very similar songs. A dialect may have evolved within Mount Fitzgerald Scenic Reserve.

Possible factors causing the patchy distribution of tits within the Reserve are discussed. This habitat may be supporting the maximum number of tits possible.

CHAPTER 1

INTRODUCTION

The Yellow-breasted tit (*Petroica macrocephala macrocephala*) is a small forest-inhabiting passerine, native to the South Island and outlying islands of New Zealand. Like the Pied tit (*P. m. toitoi*) in the North Island, its range has been reduced with the logging and burning of native forest-cover by European-man since his arrival early last century.

A review of the literature in early 1977 revealed that no detailed studies on the biology of the bird had been carried out. Therefore, an investigation with the principal aims of examining the breeding biology and behaviour of the bird throughout the year was undertaken in Mount Fitzgerald Scenic Reserve on Banks Peninsula, commencing in June 1977. The study was based on a population containing colour-banded birds.

This chapter is a general introduction to the biology of the Yellow-breasted tit, covering its phylogenetic relationships, current distribution, and reviewing the previous and current work. The various aspects of the biology investigated and the outlay of thesis are detailed, and the chapter concludes with a glossary.

1.1 PHYLOGENETIC RELATIONSHIPS

The New Zealand tits come under the following classification:

Order Passeriformes (Perching birds)
Suborder Passeres (= Oscines) (Song birds)
Family Muscicapidae (Warblers, Flycatchers, etc.)
Subfamily Muscicapinae (Flycatchers)
Genus *Petroica* Swainson, 1829.

The Yellow-breasted tit *Petroica macrocephala macrocephala* is a member of the wide-ranging Australo-Polynesian genus *Petroica*, which comprises 12 species (Macdonald, 1973). Seven species are endemic to Australia (Macdonald, *op. cit.*), two to New Guinea (Rand and Gilliard, 1967), and three to New Zealand. Two of the Australian species have, however, recently been placed in the genus *Melanodryas* (Stewart, 1977).

Within the New Zealand region, two distinct lineages are recognized - the Robins, *Petroica australis* (Sparrman) and *Petroica traversi* (Buller), which are often placed in the subgenus *Miro* (Lesson), and the Tits *Petroica macrocephala* (Gmelin). The Tits are thought to have closer affinities with the Australian members of the genus than with the Robins.

The ancestral form from which the New Zealand Tits and Robins arose is believed to be the Australian Scarlet robin *Petroica multicolor* (Gmelin). Fleming (1950) believed that the two New Zealand forms arose from two separate invasions of the same rootstock, with the ancestors of the Robins arriving in New Zealand possibly during the Pliocene, and the ancestors of the Tits probably arriving later, perhaps in the early Pleistocene. The Scarlet robin has many distinctive races throughout Australia and the Polynesian region and it is the only Australian species to show long-distance dispersal over water, reaching Norfolk Island, the New Hebrides, the Fiji Islands, Samoa and the Solomon Islands (Fleming, *op. cit.*; Mayr, 1934). Mayr described 11 subspecies, and Holyoake (1979) has recently described a new subspecies from Fiji.

After the colonizing form of the Scarlet robin reached the New Zealand region, *macrocephala* evolved. This was followed by the colonization of the outlying islands, resulting in subspeciation. Finally, differentiation occurred between the North and South Island populations when Cook Strait last became a barrier to dispersal about 15,000 years ago (Fleming, 1962). This was aided by a reduction in

flight capabilities (i.e. vagility).

The Australo-Polynesian members of the subfamily Muscicapinae are small insect-eating birds. Many take their prey on the wing, but on the whole they are not particularly efficient at, or well-adapted for, this mode of feeding. They have a wide gape resulting from the flattening of the base of the bill, which is edged with stiff bristles or vibrissae. These extend the catching area (Macdonald, 1973).

Five New Zealand subspecies are currently recognized (O.S.N.Z., 1970). These are:

Petroica macrocephala (Gmelin, 1879)

a) *P. m. toitoi* (Lesson, 1828) Pied tit.
   - North Island, Hen and Chickens, Little and Great Barrier Islands and Kapiti Island.

b) *P. m. macrocephala* (Gmelin, 1789). Yellow-breasted tit.
   - South Island, Stewart Island and outlying islets, and Solander Island.

c) *P. m. chathamensis* Fleming, 1950. Chatham Island tit.
   - Chatham Islands.

d) *P. m. dannefaerdi* (Rothschild, 1894) Black tit.
   - Snares Islands.

e) *P. m. marrineri* (Mathews and Iredale, 1913). Auckland Island tit.
   - Auckland Islands, including Adams, Enderby and Rose Islands.

Therefore, within the New Zealand region *P. macrocephala* can be thought of as a polytypic species with all forms being distributed allopatrically. The Yellow-breasted tit exhibits the most generalized form and all other subspecies can be derived from it (Fleming, 1950).

Yellow-breasted tits exhibit sexual dimorphism in plumage morphology. Males are about 120 mm in length (n = 5) and females about 115 mm (n = 10), and have the following morphological characteristics

when in adult plumage.

Male:

Head, throat, back, tail and wing coverts glossy black. Breast and underparts bright yellow. The flight feathers are a dull black with a prominent L-shaped white wing-bar. There is a white frontal spot above the beak.

Female:

Upper parts soft-brown. Breast and underparts dull yellow. The frontal spot is white and the wing-bar yellowish-brown. The female is much duller in appearance than the male.

The remaining subspecies all differ from the above description. In the Piedtit, white replaces the yellow on the breast in both sexes. The male Chatham Island tit is similar to the male Yellow-breasted tit but the female exhibits a slight tendency towards male colouration. This subspecies is also larger and has a longer tarsus. The male Auckland Island tit also has a yellow breast. The plumage of the female, however, is very similar to the male's colouration. In the Snares tit both sexes are melanistic. For further morphological details see Fleming (1950) and Oliver (1955), and Chapter 7.

1.2 CURRENT DISTRIBUTION

Because of the reduction in native forest-cover, tits are not commonly found in settled districts in which little forest is left. However, they can be found in many remaining forested areas, from rimu forest at sea level to beech forest at 1200 m, and even in the scrub above the bushline (Oliver, 1955). They are also present in second-growth forest and regenerating scrub. Those living at higher altitudes are often found along the larger, more open streams where the vegetation along the banks is more dense (St. Paul, 1976).

In some areas, however, tits are absent from apparently suitable habitats. In an example provided by Skinner (1978) for the Pied tit in the Waitakere Ranges, birds were present in the less modified bush but were absent from the regenerating *Leptospermum* scrub merging into it. This, and other examples, suggest that tits are unable to fully utilize some areas which have been extensively modified by man. Elsewhere, patches of bush may be too small to provide a suitable habitat. This was seen around my study area where a number of such patches remained uninhabited. These had an open canopy with little undergrowth and had grass growing on the ground. Bush area and structure, therefore, are probably important in determining the presence of tits. The patchy distribution of tits within an area of bush is discussed in Chapter 10.

In some parts of New Zealand the range of the tit is extending. It is commonly found in the more mature stands of exotic forest, particularly *Pinus* species, and is one of a number of native species to successfully exploit such a habitat (Jackson, 1971). The Yellow-breasted tit is commonly seen in Ashley State Forest in North Canterbury (pers. obs.) and the Pied tit is common in Kaingaroa State Forest (Gibb, 1961). Both these areas are dominated by *Pinus* species.

Figure 1.1 shows the current distribution of the Yellow-breasted tit as compiled from the results of the Bird Distribution Mapping Scheme of the Ornithological Society of New Zealand (Bull *et al.*, 1978). (Additional data come from Kelly (1972) and Wendelken (1975).) This shows that the tit is often restricted to the forested higher altitudes which are seldom frequented by man. Their absence from more settled areas suggests that they are intolerant of continuous interference from man, but can readily survive in areas which are not subject to sudden or continuous modification.

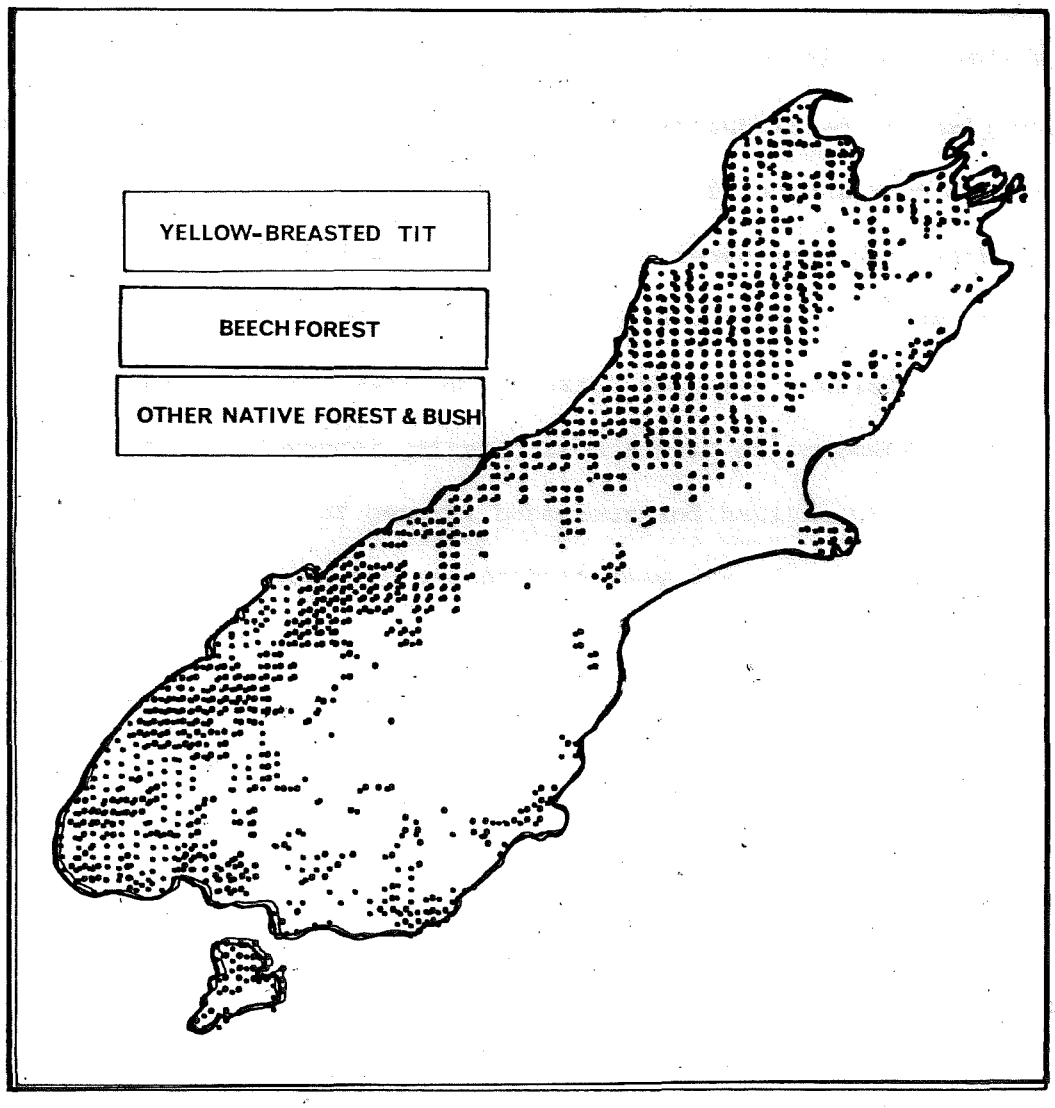


FIGURE 1.1 Distribution of the Yellow-breasted tit in relation to forest-cover.

(used and adapted with the permission of the O.S.N.Z.)

1.3 PAST AND PRESENT WORK

In common with the majority of New Zealand bush birds, very little detailed work has been carried out on the Yellow-breasted tit. Probably one of the main reasons for this is that the New Zealand bush is difficult to work in, particularly when attempting to make observations on, and follow, small birds.

Therefore, up until about the last decade the only information available on many of these species was that published by early workers in the late 1800's and early 1900's. Much of the information available on the Yellow-breasted tit falls into the above category, with a scattering of published data continuing to appear up to the present time. Unfortunately, much of the early material consists of anecdotal and piecemeal references gathered from single or scattered observations. These give examples of general behaviour and habits but do not give a detailed overall picture, and because they are often isolated observations they can be difficult to put back into context. Data published during this period cover such topics as nest placement, description of eggs and nests, breeding, food and feeding, song, some behaviour and morphological description (Potts, 1869, 1870, 1873, 1882, 1883, 1884; Buller, 1882, 1888, 1905; Barker, 1883; Reischek, 1887, and M'Lean, 1911, on the Pied tit; Smith, 1893). Oliver (1968) lists other references found in the literature before 1900.

Following this period further information appeared at irregular intervals. Guthrie-Smith (1914) added further details on breeding and behaviour, and Andersen (1926) discussed song and translated some phrases into musical notation. The most detailed account of the breeding biology of tits during this period was on the Pied tit (Wilkinson, 1930; Wilkinson, 1927; Wilkinson and Wilkinson, 1952). Parkin and Parkin (1951) and Anglesey (1957) made observations on individual nests for the

Pied and Yellow-breasted tits, respectively. Oliver (1955) summarized much of the known information, but added little new data. Soper (1976) briefly covered breeding biology and breeding behaviour, as did St. Paul (1976) for the Pied tit. Skinner (1978) discussed the status of the Pied tit in the Waitakere Ranges. Fleming (1950) published the most important work on the New Zealand Tits (and Robins) but was primarily concerned with taxonomy.

Recently there has been a resurgence of interest in the native bird fauna of New Zealand, particularly with the fate of many tracts of native forest in the balance. Concern has been raised as to the effects such clearance and modification of the habitat will have on the bush inhabitants and this in turn has led to a greater awareness of many formerly neglected species.

The amount of detailed research being carried out on members of the genus *Petroica* has increased rapidly over the last decade. However, much of this work has yet to be published. More research has taken place on the Robins than on the Tits. A population of colour-banded South Island robins in Kowhai Bush, Kaikoura, has been intensively studied over the last 10 years (Flack, 1973, 1976a, in prep. b; Powlesland, 1979). The effects of predation have also been examined (Moors, 1975, 1976; Flack and Lloyd, 1978). The endangered Chatham Island Black robin has also been studied (Flack, 1974, in prep. a; Morris, 1977). Hay (1975) analyzed the vocalizations of the New Zealand Robins and briefly covered the Tits. The function of the frontal spot and crown feathers in the Robins, and to a lesser extent in the Tits, has also been investigated (Flack, 1976b).

Only two detailed studies have been carried out on the biology of the Tits. Bisset (1978) analyzed the calls and song of the Pied tit and briefly covered social behaviour. The breeding biology and feeding

behaviour of the Snares Black tit has been investigated by Best (1975).

1.4 THE SCOPE OF THE PRESENT STUDY

The research for this thesis centred on the ecological and behavioural aspects of the biology of the Yellow-breasted tit and was based on data gathered from approximately 130 tits.

Aspects investigated covered the following topics: territorial biology, including territory maintenance and the movements of banded birds (Chapter 4); nests and nest site (Chapter 5); breeding biology (Chapter 6); plumage and moult (Chapter 7); feeding biology, including feeding behaviour and the types of food taken (Chapter 8); and the vocal repertoire of the tits (Chapter 9). Mist netting results are presented in Chapter 3 while in Chapter 10 possible factors influencing the distribution of tits in different habitats are considered. All vocalizations mentioned in the text are discussed in Chapter 9.

Detailed field-work was carried out from mid-June 1977 to March 1979, with further observation and mist netting continuing at irregular intervals up to August 1979.

1.5 SOME TERMS DEFINED

a) Throughout the remainder of this thesis the term "tit" or "tomtit" refers to the Yellow-breasted tit. Where another species is mentioned, its full common or scientific name is given.

b) The letters O.S.N.Z. are an abbreviation for the Ornithological Society of New Zealand. When Nest Record cards are mentioned, this is in reference to the Society's Nest Record Scheme.

c) Notation such as 12-9-77 refers to the 12th day of the ninth month of 1977.

d) dependent fledgling: a fledged bird still being fed by its parents.

e) juvenile: an independent fledgling which has not moulted into adult plumage.

f) immature: a bird of the year in adult plumage.

g) adult: a bird present in the current breeding season which was present or fledged in a previous breeding season.

CHAPTER 2

STUDY AREA AND METHODS

2.1 INTRODUCTION

The location, topography, climate and vegetation of the study area and its environs are described in this chapter. The history of the vegetation of the surrounding region is discussed in some detail because it may be influencing the current distribution and abundance of tits in the area. This aspect is discussed more fully in Chapter 10.

The chapter ends with a short discussion on the methods of study employed. Details of specific methods are given in the relevant chapters.

2.2 THE STUDY AREA

2.2.1 Location

The work was carried out in Mount Fitzgerald Scenic Reserve, Banks Peninsula, 65 km south-east of Christchurch (Figure 2.1a). The Reserve lies on the southern slope of Mount Fitzgerald in the Hikuika (or Terawera) Valley, 8 km north-east of Little River. It is one of about six scenic reserves which lie along or near the central high ridge of Banks Peninsula. There are three other reserves within one kilometre of Mount Fitzgerald, and a fourth about two kilometres away (Figure 2.1b). There are also small patches of bush and scrub scattered throughout the area.

Figure 2.1

2.1a Study area is located within the rectangle.

2.1b Exact location.

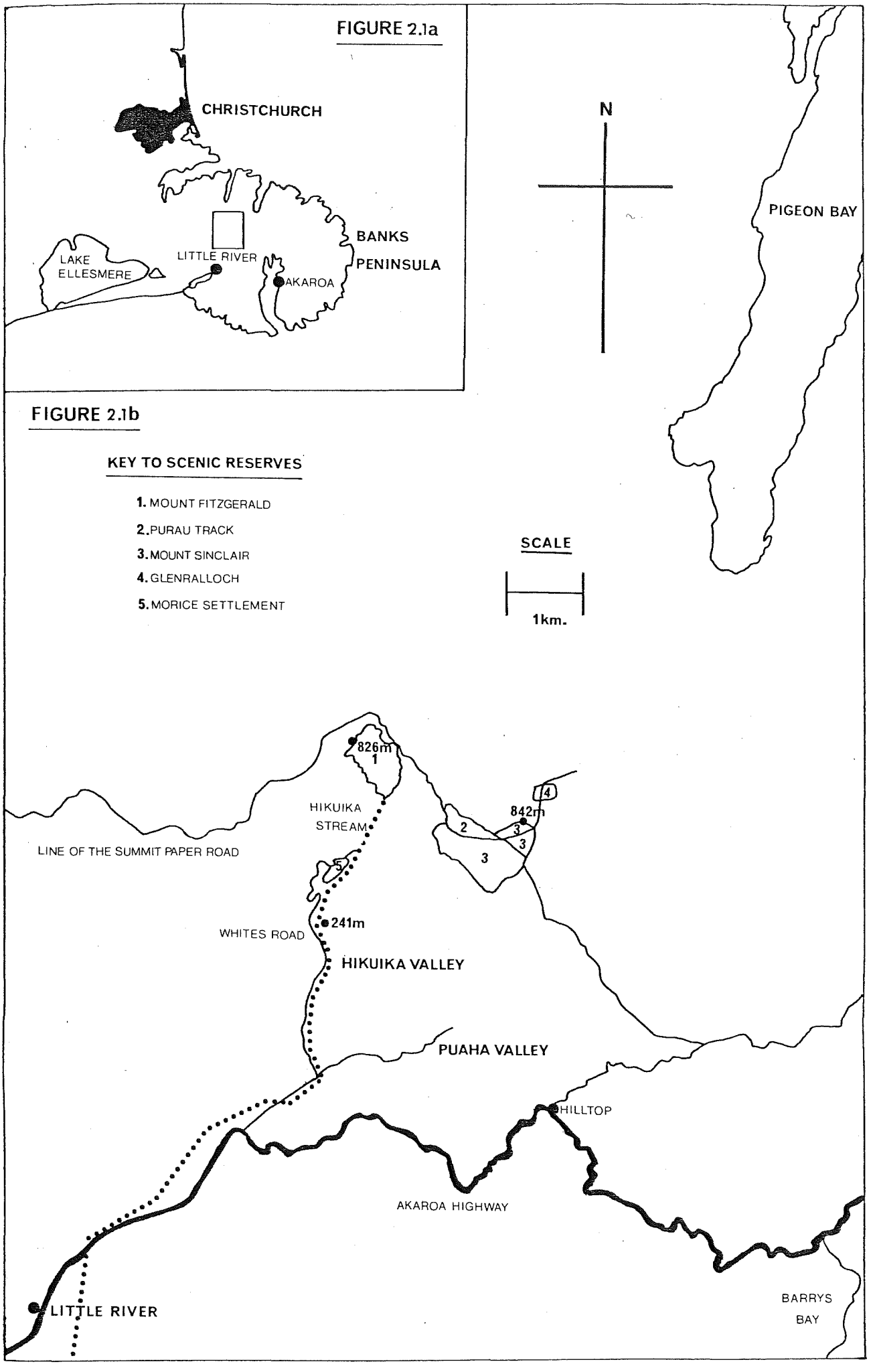


FIGURE 2.1a
CHRISTCHURCH
LAKE ELLESMERE
LITTLE RIVER
AKAROA
BANKS PENINSULA
N
PIGEON BAY
FIGURE 2.1b
KEY TO SCENIC RESERVES
1. MOUNT FITZGERALD
2. PURAU TRACK
3. MOUNT SINCLAIR
4. GLENRALLOCH
5. MORICE SETTLEMENT
SCALE
1km.
826m
1
HIKUIKA STREAM
842m
LINE OF THE SUMMIT PAPER ROAD
241m
WHITES ROAD
HIKUIKA VALLEY
PUAHA VALLEY
HILLTOP
AKAROA HIGHWAY
LITTLE RIVER
BARRYS BAY

Access to the Reserve is from Whites Road which runs off the Akaroa Highway. From the end of Whites Road there is a one kilometre walk up to the study area. Access can also be gained from along the Summit paper road.

Two 3-day visits were made to Mount Fyffe State Forest at Kaikoura to gather additional data on the behaviour, calls and song of the local Yellow-breasted tits.

2.2.2 History of the study area

The Reserve is one of numerous, small forested areas remaining on Banks Peninsula. These stands are now so modified that it is difficult to reconstruct a clear picture of the virgin forest of the early 19th century (Holloway, 1954).

Before European man arrived on Banks Peninsula, in the early to mid 19th century, it is estimated that about 50% of the total area of 116,000 hectares was forest-clad (Laing, 1918; Akaroa Mail Co., 1940; McLintock, 1966). The forest cover was not continuous, but was densest in the central region of the peninsula and those areas exposed to the south (Milligan, 1941). In such areas, only a few bald peaks showed through the forest cover (e.g. Mounts Fitzgerald, Sinclair and Herbert) (Laing, 1918). The drier slopes with a northern aspect were covered in tussock grassland and the dead remnants of former forest (Holloway, 1954). The dominant forest-type on the peninsula was a podocarp-broadleaf mix with a few isolated patches of beech forest (*Nothofagus* spp.) (Laing, 1913, 1918). (The term broadleaf refers to the many dicotylous hardwood trees found in association with the softwood podocarps of the mixed forests (Robbins, 1961).)

By 1870 less than 25% of the original forest cover remained and by 1910 it had almost disappeared (Milligan, 1941). The area around Little River and the valleys to the north-east of it (including the

study area) were among the last virgin areas to be cleared of their cover. In 1880 the area around Mount Fitzgerald was still heavily forested, but from the mid 1880's onwards timber was cut out of this area (Petrie, 1963) and continued to be removed up to about 1900 (Akaroa Mail Co., 1940).

Two main practices were used to clear the land. The method used depended on the purposes for which the land was needed. If the land was required immediately for farming, then the smaller trees and undergrowth were cut-down, but the larger trees, including the podocarps, were left standing. The vegetation was then burned, leaving thousands of upright dead trees in a blackened and scorched condition. Such trees can still be seen in the higher regions around the study area today. If the land was to be used for logging, all the millable trees were removed and those remaining were burned. The land was then used for farming (Appendix to the Journal of the House of Representatives of New Zealand, 1877).

Today only 2500 ha of bush remain on Banks Peninsula (Petrie, 1963), less than 5% of the original cover.

By 1905, when the land to the south of Mount Fitzgerald was broken up into smaller farms, the area surrounding the bush remnant on Mount Fitzgerald was described as "all cleared bush land, now in cocksfoot grass" (Department of Lands, 1905). This condition had probably prevailed since at least the early 1890's. Figure 2.3a shows the appearance of the area at this time.

The bush remnant on Mount Fitzgerald was gazetted as a reserve in 1907 (Kelly, 1972). However, despite being superficially intact, it had been burnt through and logged of the prime prodocarps in the lower regions so that it was mainly a broadleaf forest with a few remnant podocarps. Evidence of fire can still be seen on some of the larger podocarps today.

A Lands and Survey aerial photograph taken in 1941 showed that

some areas along the streams had still not regenerated by this time. A further aerial photograph taken in 1976, however, revealed that all these areas were now covered in vegetation (Figure 2.2).

Because only the east side of the reserve is fenced, stock damage has taken place, but it varies with access and terrain. This has resulted in the undergrowth being extensively modified by sheep and, in particular, cattle.

2.2.3 Bird life

Before the Banks Peninsula forests were logged they contained large numbers of nearly all the native South Island bush birds (Stead, 1927). Species formerly found in this area included parakeets (*Cyanoramphus* spp.), kakas (*Nestor meridionalis*), native thrushes (*Turnagra capensis*), saddlebacks (*Philesturnus carunculatus*), kokakos (*Callaeas cinerea*), yellowheads (*Mohoua ochrocephala*), bush wrens (*Xenicus longipes*), moreporks (*Ninox novaeseelandiae*) and tuis (*Prosthemadera novaeseelandiae*) (Stead, 1927; Akaroa Mail Co., 1940).

The surviving bush is therefore, an important refugium for a declining bush bird community. Species surviving in the area around the study area include tits, bellbirds (*Anthornis melanura*), rifleman (*Acanthisitta chloris*), brown creepers (*Finschia novaeseelandiae*), fantails (*Rhipidura fuliginosa*), silvereyes (*Zosterops lateralis*), grey warblers (*Gerygone igata*), pigeons (*Hemiphaga novaeseelandiae*) and shining cuckoos (*Chalcites lucidus*). There have been occasional reports of sightings of robins in Okuti Valley near Little River (W. Buckland, pers. comm.).

2.2.4 Mammalian inhabitants

The possum *Trichosurus vulpecula* is very common in the Reserve. Defoliation of pate (*Schefflera digitata*) and five-finger (*Neopanax arboreum*) has resulted from their activities.

Figure 2.2

An aerial photograph of Mount Fitzgerald Scenic Reserve and its environs, taken in 1976. The radiating fingers of bush in the west and north-west follow the main streams in the area. (Reproduced with permission of the Department of Lands and Survey.)

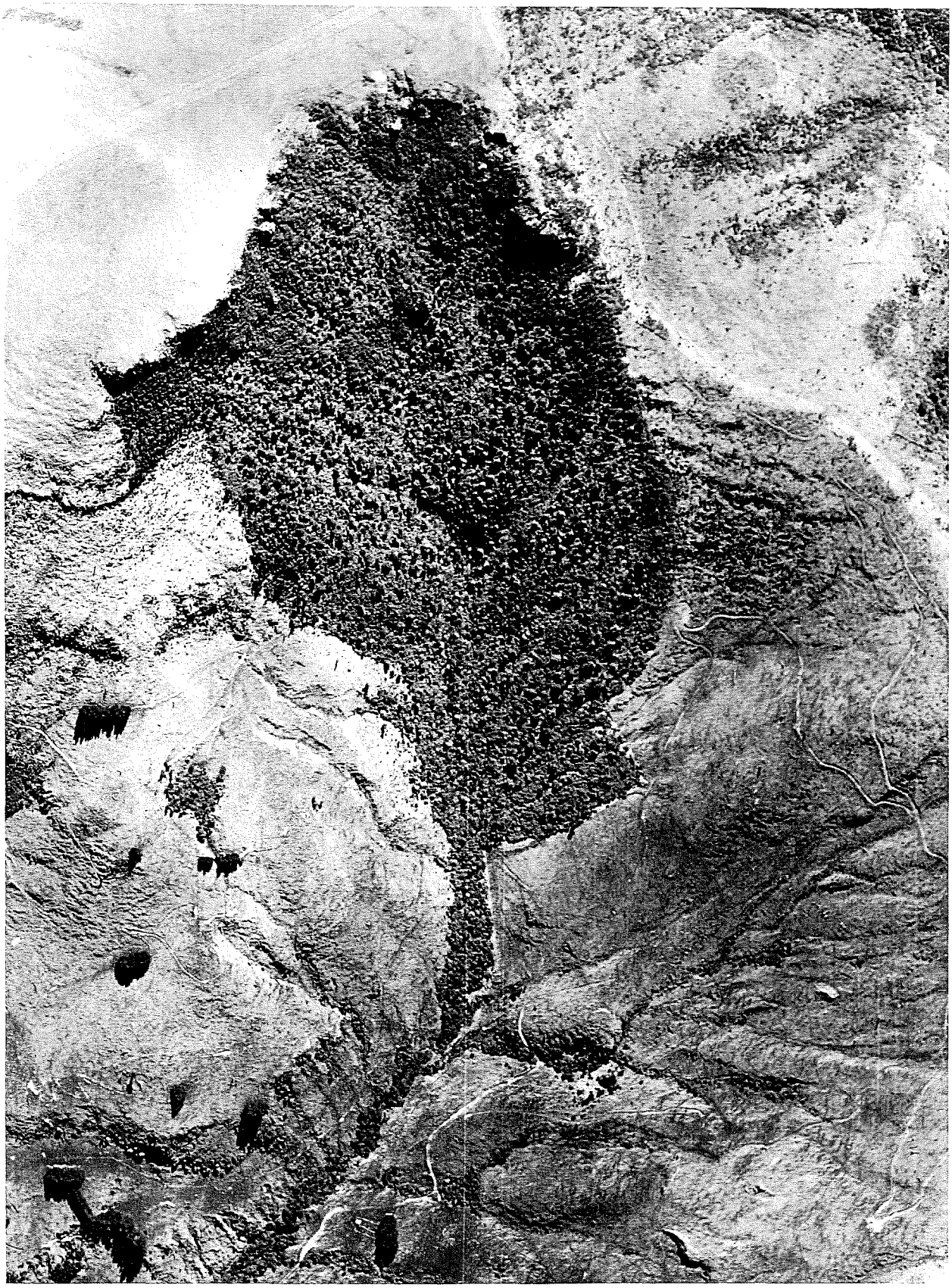


Figure 2.3a.

The appearance of the area around Mount Fitzgerald in about 1905 (Mount Fitzgerald in the central background).

Figure 2.3b

The Reserve as it appears today.

Morice Settlement.—The Hikuika Valley with Mount Fitzgerald in background.

Rats (*Rattus* sp.) and probably mice (*Mus musculus*) are also present. Hares (*Lepus europaeus*) were seen in the central areas of the Reserve. Mustelids - weasels (*Mustela nivalis*) and stoats (*M. erminea*) were often heard rustling about in the leaf litter, but were only rarely seen.

2.2.5 Topography and climate

Mount Fitzgerald Scenic Reserve is 43.7 ha in area and fills the head of a small, steep gully, surrounded at the top by a semicircle of bluffs (Figure 2.3b). On the less steep slopes there is a coating of loess. There is a small, subalpine element growing on the highest bluffs (Laing, 1923).

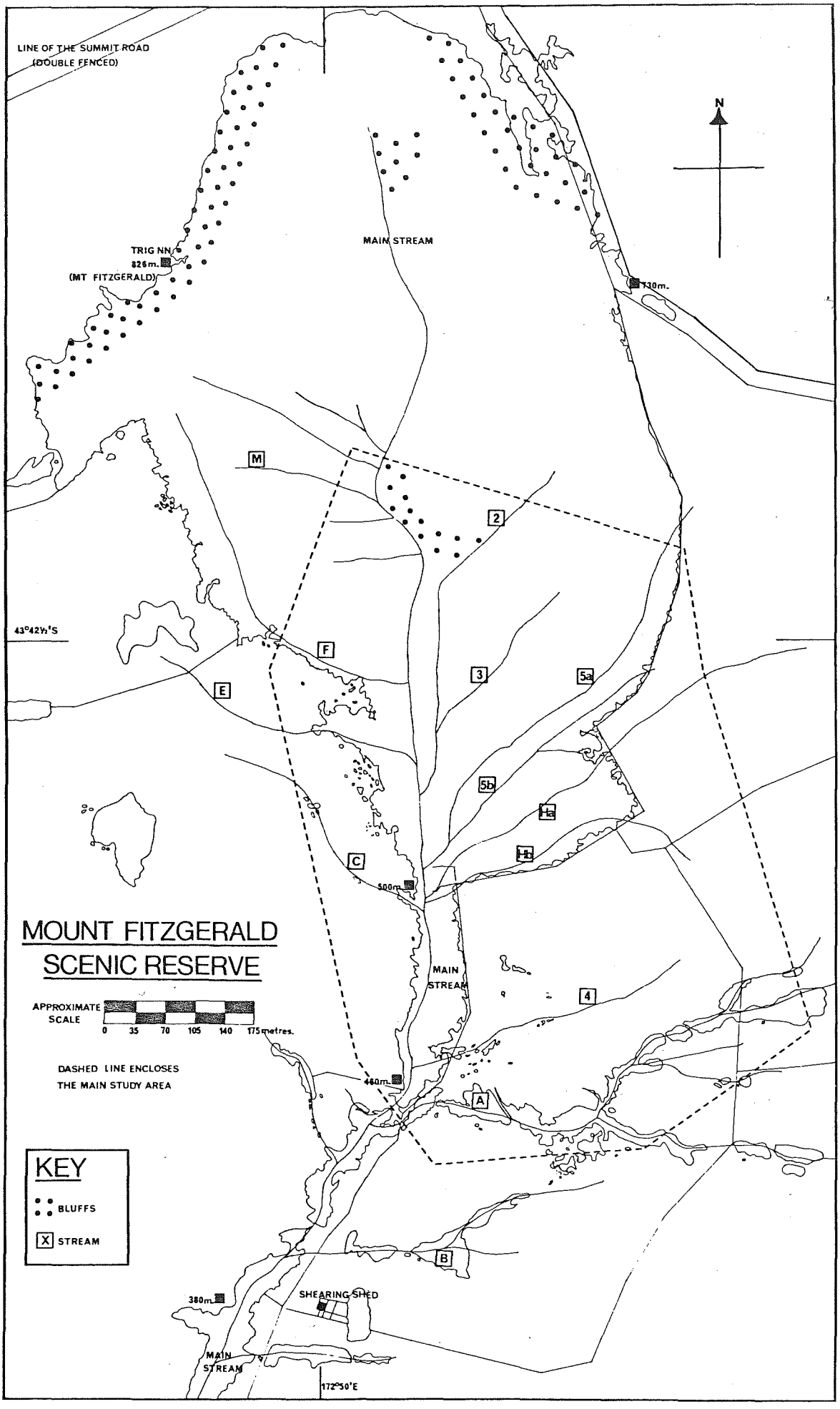
The country surrounding the Reserve is steep and hilly, a result of the volcanic origin of Banks Peninsula (see Figure 2.2). Because of the high annual rainfall (1400 mm approx.) it has been classified as the second best montane habitat on the peninsula after Herbert Peak Scenic Reserve (Kelly, 1972). The Reserve is exposed to the south and is often covered by low cloud and mist during the winter. Snow falls occasionally during the winter and spring, but remains on the ground for no more than a week at the most, usually less. The bottom boundary of the Reserve lies at 500 m altitude with the peak of Mount Fitzgerald at 826 m being the highest point (Figure 2.4).

The area is well-served by streams with the main stream (or Hikuika Stream) running through the entire Reserve and being fed by a number of smaller streams. The main stream continues below the Reserve, passing through Morice Settlement Scenic Reserve about one kilometre downhill. Bush-lined, smaller streams feed into it from the open fields.

Only streams 2, 5a, Ha, A and B run throughout the year, the remainder drying up over the summer. Streams Hb and 5b run underground for much of their course, particularly during the summer.

Figure 2.4

Diagrammatic representation of Mount Fitzgerald Scenic Reserve with the location of the study area indicated.


LINE OF THE SUMMIT ROAD
(DOUBLE FENCED)
N
MAIN STREAM
TRIG NN
826m.
(MT FITZGERALD)
730m.
M
2
43°42½'S
F
E
3
5a
5b
Ha
Hb
C
500m.
MOUNT FITZGERALD
SCENIC RESERVE
APPROXIMATE
SCALE
0 35 70 105 140 175 metres.
DASHED LINE ENCLOSES
THE MAIN STUDY AREA
MAIN
STREAM
4
460m.
A
KEY
BLUFFS
STREAM
B
380m.
SHEARING SHED
MAIN
STREAM
172°50'E

Within the study area (Figure 2.4) the main stream flows through two different terrains. From its source above the study area, down to the bluff in the middle of the Reserve, it has a steep descent and shallow banks. Below this area it has a much slower rate of descent with banks up to five metres high in some places. The bed is composed of boulders, shingle and alluvium, and is choked with logs and debris in many places. The size and distribution of streams within the study area may have an effect on the density and distribution of tits in some areas (see Chapter 10).

Because the higher parts of the Reserve were so steep and difficult to move through, only the less steep terrain, which was situated in the lower part of the Reserve, was included in the study area. Some bush below the Reserve was also included so that the total area of bush in the study area covered about 16 hectares.

2.2.6 Vegetation

As a result of the extensive logging and burning which took place late last century, much of the vegetation present today has regenerated within the last 80-90 years, resulting in a highly modified patch of bush.

Within the study area, the tree fuchsia, *Fuchsia excorticata*, and pepper tree, *Pseudowintera colorata*, dominate and form much of the canopy. The tree fuchsia is one of the few winter-deciduous native trees (Wardle, 1978). Scattered throughout the area are podocarps, usually being clustered along the major streams. The majority are pre-European, and many are dead or dying. *Griselinia littoralis* (broadleaf) is the other large tree species present, and is evenly dispersed throughout the area.

The canopy height varies between about 3 and 12 metres, with the majority of trees lying in the 6 to 8 metre range. Besides the tree fuchsia and pepper tree, several other species commonly form part

of the canopy. These include the five-finger *Neopanax arboreum*, lemonwood *Pittosporum eugenioides*, black matipo *P. tenuifolium*, and *Pennantia corymbosa*. In areas where fuchsia is less dominant the canopy is higher.

Rising above the canopy are the emergent trees, consisting mainly of Hall's totara *Podocarpus hallii*, which can grow up to 20 metres tall but was usually in the 12-18 metre range, and broadleaf, growing up to about 12 metres. Kahikatea *P. dacrydioides*, and matai *P. spicatus* were less common. These species would have probably formed the canopy before the area was logged.

The middle storey was absent in some areas, but where present it was often dominated by pepper trees. Other common species in this layer were *Coprosma rotundifolia*, pate *Schefflera digitata* and the regenerating canopy species. All these species could be found in the canopy if the canopy height was low (i.e. 3-4 metres).

Ground cover varied from bare leaf litter to a mixture of ground-ferns consisting of *Polystichum* spp., *Blechnum* spp., and *Leptolepia novae-zelandiae* near the streams.

The tree-fern *Cyathea smithii* had a patchy distribution within the study area, being found in the canopy or middle storey. Climbing vines were common, being distributed throughout the vegetation profile.

Mount Fitzgerald Scenic Reserve is surrounded by pasture dominated by browntop *Agrostis tenuis* and cocksfoot *Dactylis glomerata*. The western bush edge contains a mixture of species including scattered *Leptospermum* sp., *Coprosma parviflora*, regenerating podocarps, and shield fern *Polystichum richardii*. Totara logs are scattered throughout the area. The eastern bush edge is dominated by shield fern at the higher altitudes with only slight regeneration of podocarps and pepper trees. This area is also strewn with totara logs.

Appendix 1 lists the dominant species in each vegetation layer. Kelly (1972) gives a more detailed species list.

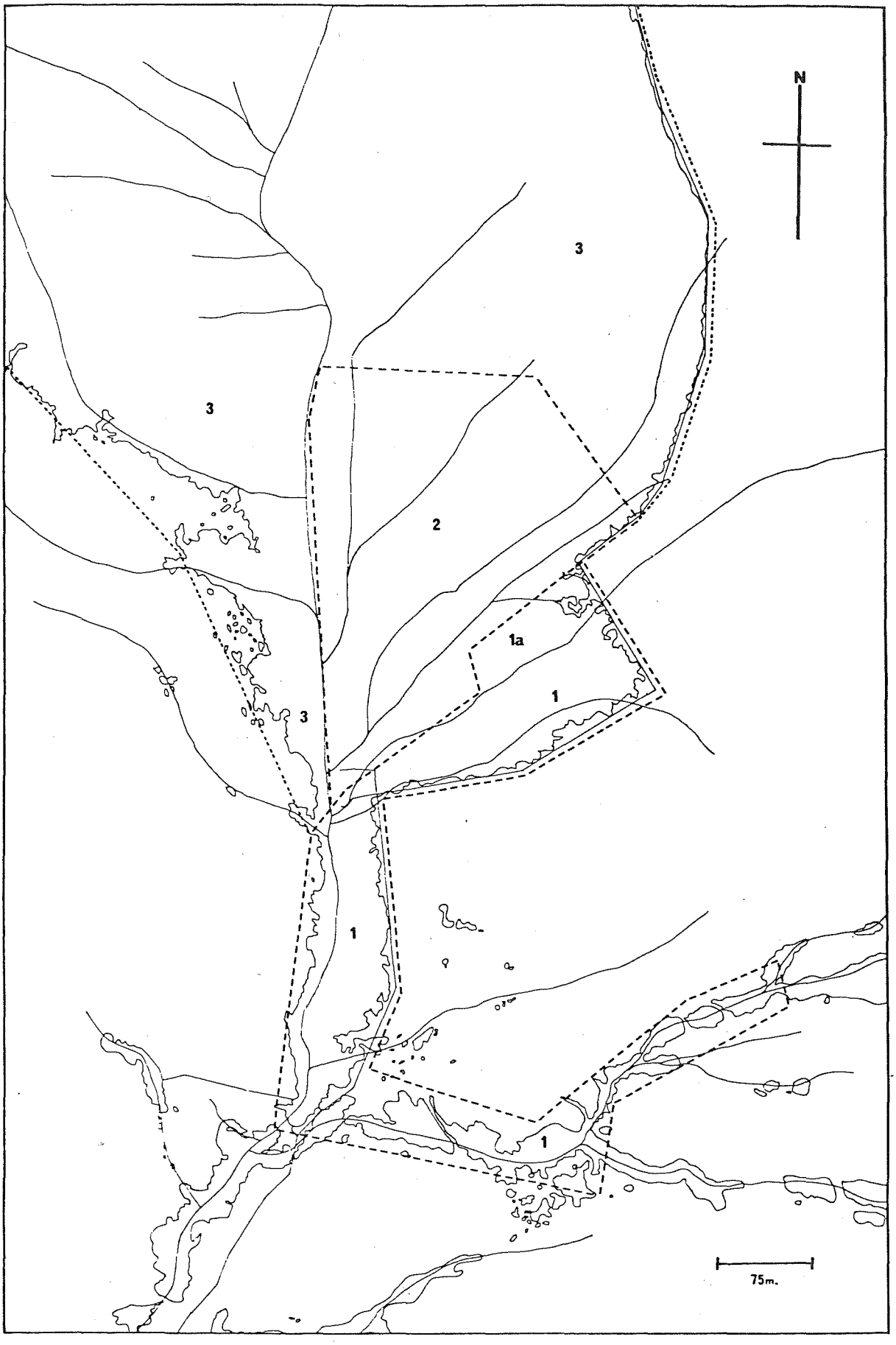


FIGURE 2.5 Vegetation patterns within the study area

Because of the differing vegetation regeneration patterns, three main areas can be recognized in the study area. These are outlined in Figure 2.5. Examples of vegetation in the ground-storey, and beneath the canopy, are illustrated in Figures 2.6a and b.

Area 1

Vegetation in this area underwent the greatest destruction at the end of the last century and has taken the longest time, of the three areas, to regenerate. The dominant emergent tree is the narrow-leaved lacebark *Hoheria angustifolia* which grows up to a height of about 10 metres. This is the only area in which it is common. Emergent podocarps and the broadleaf are rare. Tree fuchsias and pepper trees still dominate the canopy, however.

The area is characterized by dense growth on the forest floor, consisting of ground-ferns and regenerating tree species, with little evidence of grazing by sheep and cattle. Area 1a, bounded by stream Ha, contains the densest regeneration. All the broadleaf species mentioned previously, as well as the podocarps, can be found here, so that an almost inpenetrable barrier of vegetation, with little separation between the canopy and lower layers, is formed.

Area 2

This area covers most of the study area, and conforms to the general vegetation structure described previously. As a result of the continual browsing by cattle, the unpalatable pepper tree is the only common regenerating species present. More broadleafs and podocarps are commoner in this vegetation type than in area 1. The canopy height increases towards the back of this area where fuchsia becomes less dominant.

Figure 2.6a

Vegetation beneath the canopy, dominated by fuchsias and pepper trees. The large tree to the right is an emergent lancewood (*Pseudopanax crassifolium*).

Figure 2.6b

The ground-storey, dominated by ground-ferns. Note the climbing vines which are common throughout the study area.

Area 3

This area is characterized by having a steeper terrain and a greater number of emergent podocarps than the other areas. However, the commonest canopy species is still tree fuchsia. Regeneration is patchy, as loose rocks cover much of the ground surface. Of the three areas, area 3 has been the least modified by the influences of man.

The most modified parts of the study area, therefore, were located in the less steep areas, typically in the front part of the Reserve. The least modified areas were located in the steeper, less accessible areas towards the back of the study area.

2.3 METHODS

Two methods were used to gather information. These were mist netting and observation.

Because the study was to be based on a population of birds in which individuals could be recognized, mist nets were used to capture the birds for banding. Morphological details were gathered at the same time. Mist netting results are presented in Chapter 3.

When a visit was made to the study area, the behaviour, movements and, if possible, the identification of all birds encountered were noted down for later analysis.

Birds were followed for several hours at a time if sequential behaviour was being studied. When individuals were being followed, or nests were being searched for, most of the study area could be covered in a day.

The frequency of visits to the study area depended on the weather. During the breeding season, visits were made on up to five days in the week, with usually no more than one or two days elapsing between visits.

During the winter, fewer trips were made because of the weather, with two to three weeks sometimes elapsing between trips. If the weather was fine, visits were made every three to four days. Trips usually lasted between five and nine hours.

CHAPTER 3

MIST NETTING RESULTS

3.1 INTRODUCTION

The use of mist nets to capture birds for measurement and banding is a well-established and successful procedure. Mist nets are particularly suitable for capturing small, fast-moving passerines in forested areas, permitting workers to plot the movements of banded birds and to estimate the population sizes of different species (MacArthur and MacArthur, 1974). Estimates of population size based upon banded birds and their subsequent resighting or recapture have proven to be more accurate than those based upon sightings of unbanded birds (e.g. Stamm *et al.*, 1960). The presence of territorial and non-territorial individuals of a species during the breeding season can also be established using mist nets (e.g. Thompson, 1977).

Despite their ease of use, mist nets have rarely been used within the New Zealand region for capturing and banding native passerines for population studies. There are several reasons for this. Much of New Zealand's native bush is dense, and it is difficult to erect mist nets in suitable sites and then to follow banded birds through thick undergrowth. However, recently Gill (1979) and Powlesland (1979) have completed research on the Grey Warbler and South Island robin respectively, and much of their work was based on banded birds captured in mist nets. A further study using mist nets, on the breeding biology and social behaviour of colour-banded Brown Creepers, is currently under progress in Kowhai Bush, Kaikoura (J. Cunningham, pers. comm.).

Successful studies can be carried out on unbanded bush birds, for example Gray (1969) on the breeding biology of the Rifleman, Best (1975) on the breeding biology and feeding behaviour of the Snares Black tit, and Bisset (1978) on the vocalizations of the Pied tit, but the aspects of the biology of a species which can be investigated are limited. This is due to the difficulties in positively identifying individual birds when they move away from the areas in which they are usually found. In contrast, birds with a unique combination of coloured bands can be monitored over the yearly cycle, allowing seasonal movements, territorial biology and the behaviour of individuals to be followed.

Because the present study was to be based on a population of tits in which at least a proportion of the birds were banded, mist netting was an important part of the work. Netting was carried out from June 1977 to late September 1977; late January 1978 to June 1978; and February 1979 to May 1979. To avoid possible interference with breeding activities netting was discontinued during the breeding season.

This chapter is based on the mist netting results and discusses the netting techniques, and the standard measurements taken from the birds captured. It concludes with a discussion of the results.

3.2 METHODS

3.2.1 Mist netting

Mist netting was carried out in two different types of site within the study area - in the bush and on the bush edge. Netting trials during June and July 1977 revealed that the location of the nets was the most important factor governing the capture rate of tits, and that some parts of the study area were more suited to the use of nets than others.

The vegetation profile determined where nets could be placed.

Where the canopy was low (4-6 m), the side-branches of the trees formed a layer 2-3 m above the ground, thus restricting the height to which the nets could be raised. The denseness of the subcanopy and shrub layer was also important. The limitations imposed by the nature of the vegetation were most evident in Area 1 of the study area (see Figure 2.5), which contained the densest and most recent regeneration. Only about six netting sites were available in this area.

Apart from the constraints imposed by the vegetation, the most important factor determining the placement of nets was the presence of tits. Nets were erected wherever tits were known to be present, if suitable sites could be found. Occasionally, however, nets were erected in areas where tits were thought to be absent to make sure that such was the case. This served as a check on whether all the birds present in an area could be detected by sight, or through vocalizations. Netting was carried out throughout the study area.

In addition, nets were placed along the edges of the study area either at an angle to, or parallel with, the bush edge. They were also erected between closely spaced tongues of bush. Nets were used in these sites only if tits were known to be present because otherwise too much time was spent dealing with captured birds of other species which frequented the bush edge. Netting in this area was also avoided after the breeding season when flocks of species such as silvereyes and redpolls formed.

From observation it soon became apparent that a pair of tits concentrated their activities in only part of their territory at any one time, in periods varying between a few days and several weeks. This pattern was present throughout the year. Knowledge of the sedentariness of individual birds allowed nets to be erected in the areas they frequented, both in the bush and along the bush edge. Mist netting was carried out more often in areas in which tits were frequently seen or

heard, than in those where they were rarely seen.

After the nets were erected a tape-recording of the song of a tit was sometimes played. Usually this would result in many tits in the immediate area flying in to investigate the source of the song, and in so doing fly into the net. This procedure was used sparingly, as tits in the area quickly became habituated to the same song after a few days and ceased to respond. Therefore, normally nets were erected and left without attempting to attract the tits. Often they avoided the nets by making last-second changes of direction.

Decoy male tits were also constructed and placed near the nets. However, the capture rate of birds was not high enough to be able to gauge the response of birds towards the decoys, so they were not persevered with. Bisset (1978) found that male Pied tits reacted to a decoy by making short, rapid flights about it, and that females ignored it.

Netting was most successful in areas shaded from direct sunlight and sheltered from strong, gusty winds. Because tits moved about throughout the day, netting success was not confined to any particular period of the day. Up to five nets were used simultaneously and all were checked every 30-45 minutes. The nets used had a mesh size of 31.75 mm (1.25") and were of the following dimensions: 2×5.5 m long $\times$ 2.74 m high, 2×12.2 m long $\times$ 2.13 m high and 1×5.5 m long $\times$ 2.13 m high.

Detailed discussion on mist netting techniques can be found in Low (1957), Stamm *et al.* (1960) and Wilson *et al.* (1965).

3.2.2 Banding and measurement of birds

Netted birds were removed from the net and placed in holding bags. Each tit was weighed in the bag, removed, and fitted with a numbered metal band and up to three coloured plastic bands, giving a unique colour combination. Native birds of other species were banded with a

numbered metal band only; individuals of introduced species were measured but not banded.

A set of standard measurements was taken from each tit after noting the sex and, if possible, the age. The measurements consisted of the following:

Wing length - from the tip of the longest primary to the anterior edge of the wrist joint.

Tail length - from the tip of the longest tail feathers to just below the vent where the feather bases emerge from the skin.

Bill length - from the tip of the beak to where the beak emerges from the feathers on the forehead.

Bill width and depth - measured where the beak emerges from the feathers on the forehead.

Vibrissae (whiskers) - the longest vibrissae were measured.

Total length - from the tip of the tail to the tip of the beak, with the bird lying ventral surface up, in the palm of the hand.

Middle toe - measured with the toe sitting on a flat surface, from its base at the middle of the metatarsal joint to where the claw emerges.

Middle and hind claws - from the tip of the claw to where it emerges from the toe. This measures the chord of the claw.

Tarsus (tarsometatarsus) - the foot was bent downwards and the tarsus measured from the metatarsal joint with the middle toe, to the midpoint of the joint between the tibia and metatarsus.

Spot width - the widest diameter was measured.

Spot depth - the depth from the top of the beak to the top of the spot - this was a variable measurement due to the way the spot was displayed at the time.

In addition, the colour of the bill, iris, legs, soles of the feet, and dorsal and ventral plumage was noted. Apart from spot width and depth, all the above measurements were taken from the other species netted also.

Total length and wing length were measured to the nearest millimetre, with a wooden rule with a metal stop-plate attached at one end. A 30 g Pesola balance was used to weigh birds to the nearest half gram. Heavier birds (e.g. bellbirds) were weighed on a 100 g Salter balance. All other measurements were made with a pair of Vernier calipers in millimetres, to one decimal place. Further details on the measurement of birds can be found in Gurr (1948).

3.3 RESULTS

Between mid-June 1977 and mid-May 1979, 33 tits (16 males and 17 females) were captured; 32 in mist nets and one, a young male close to fledging, by hand as he attempted to escape from the nest. Six birds were recaptured; five once and one bird three times (see Table 3.1). Times between recaptures ranged from one day to 11 months. Not all the birds were recaptured in the same area as their original capture. Recaptured birds provided information on movements (Chapter 4), and the timing and duration of the moult in adults and juveniles (Chapter 7).

Table 3.1. Recapture dates of banded tits

Bird no.	Capture date	Recapture date
Female 111	11-9-77	12-9-77 6-4-78 8-2-79
Male 113	12-9-77	12-3-78
Male 126	29-1-78	8-5-78
Male 128	30-1-78	18-2-78
Female 141	15-2-78	1-4-78
Male 149	10-3-78	18-3-79

All tits captured were classified as male or female in juvenile or adult plumage. They were classified according to plumage type rather than as adults and juveniles *sensu stricto* because the actual maturity of some birds could not be determined after the breeding season had ended. This occurred when juveniles moulted into adult plumage thus becoming indistinguishable from the adult birds. Therefore, both immature and adult birds in adult plumage were present. However, birds in juvenile plumage which attained adult plumage early after the end of the breeding season were distinguishable from non-moulting adults due to their brighter ventral colouration and less-worn plumage.

The number of tits captured during the different periods of the year are given in Table 3.2.

Table 3.2 Numbers of tits in each plumage class, and period of year when captured.

	Adult plumage		Juvenile plumage	
Time period	Males	Females	Males	Females
mid-June 1977 to late September 1977	5	4	0	0
1977 Breeding Season	0	0	1*	0
Late January 1978 to June 1978	3	6	5	4
1979 Breeding Season	0	0	0	0
late January 1979 to mid-May 1979	0	2	2	1
Total	8	12	7	5

* not included in column total or statistical analysis (see text for explanation).

Birds in juvenile plumage starting to moult into adult plumage are included in the juvenile plumage classes. The unfledged male banded

during the 1977 breeding season is not included in the column total as he was excluded from later statistical analysis.

Statistical analysis was carried out using the S.P.S.S. system of computer programmes (Nie *et al.*, 1975), run through a Burroughs B6718 computer. The raw data on which this analysis is based are tabulated for each tit in Appendix 2, which also includes the capture date and state of the plumage for each bird.

Table 3.3 summarizes the mean, standard error and sample size for each of the 14 variables in each plumage class.

Table 3.3. Summary of variables measured.

Variable		Adult plumage Males	Adult plumage Females	Juvenile plumage Males	Juvenile plumage Females
Weight	$\bar{X}$	11.25 ± 0.25	11.12 ± 0.17	11.93 ± 0.83	11.80 ± 0.20
	n	8	12	7	5
Wing	$\bar{X}$	73.37 ± 1.03	71.17 ± 0.67	74.43 ± 0.30	69.80 ± 0.73
	n	8	12	7	5
Tail	$\bar{X}$	49.96 ± 0.82	46.69 ± 1.16	50.60 ± 0.55	45.88 ± 1.10
	n	8	12	7	5
Bill length	$\bar{X}$	10.27 ± 0.16	9.76 ± 0.18	9.67 ± 0.17	10.26 ± 0.43
	n	8	12	7	5
Bill width	$\bar{X}$	4.41 ± 0.14	4.07 ± 0.08	4.33 ± 0.07	4.50 ± 0.14
	n	8	12	7	5
Bill depth	$\bar{X}$	3.25 ± 0.06	3.20 ± 0.07	3.39 ± 0.09	3.10 ± 0.06
	n	8	12	7	5
Whiskers	$\bar{X}$	10.57 ± 0.28	9.35 ± 0.19	8.59 ± 0.51	9.54 ± 0.55
	n	3	8	7	5
Total length	$\bar{X}$	119.50 ± 1.50	115.25 ± 1.47	120.00 ± 1.15	115.00 ± 1.00
	n	2	8	3	2
Middle toe	$\bar{X}$	13.00 ± 0.40	12.57 ± 0.35	12.89 ± 0.54	11.84 ± 0.48
	n	8	11	7	5
Middle claw	$\bar{X}$	5.37 ± 0.25	5.12 ± 0.10	5.47 ± 0.13	5.16 ± 0.07
	n	5	11	7	5
Hind claw	$\bar{X}$	6.51 ± 0.19	6.73 ± 0.21	6.74 ± 0.15	6.16 ± 0.15
	n	8	11	7	5
Tarsus	$\bar{X}$	25.29 ± 0.50	25.24 ± 0.37	25.16 ± 0.59	25.18 ± 0.58
	n	8	11	7	5
Spot width	$\bar{X}$	6.66 ± 0.24	6.24 ± 0.19	5.30 ± 0.16	5.35 ± 0.20
	n	8	11	7	4
Spot depth	$\bar{X}$	2.57 ± 0.21	1.54 ± 0.12	1.93 ± 0.37	0.97 ± 0.21
	n	8	11	6	4

$\bar{X}$ = mean, n = sample size.
All measurements in millimetres. Weight in grams.

To test for statistically significant intra- and intersexual differences, t-tests were performed between the different plumage and sexual groups for each variable measured. A two-tailed test of significance was used, with a probability value of less than 0.05 being accepted as significant. Comparisons were made between the following plumage classes:

a) adult and juvenile male,
b) adult and juvenile female,
c) adult male and female,
d) juvenile male and female, and
e) all males and females.

A t-test was used in preference to a Mann-Whitney U test because the number of birds captured was considered to be a representative and sufficiently large enough sample of the total number of tits inhabiting the study area.

Significant results are given in Table 3.4.

Table 3.4. Some statistically significant results from inter- and intrasexual comparisons.

Group comparison	Variable	Significance (p)
a	Spot width	0.001
b	Spot width	0.022
	Spot depth	0.028
c	Spot depth	< 0.001
d	Wing length	< 0.001
	Tail length	0.002
e	Wing length	< 0.001
	Tail length	0.001
	Total length	0.022

The comparison between all males and all females gave two highly significant results for wing length and tail length. Figure 3.1 illustrates the separation between the sexes for these two variables.

Figure 3.1

Scattergram of wing length vs tail length for all males and all females

▼ females

▽ males

The mean ± 2 standard errors is also plotted for each variable.

Female

wing $\bar{X}$ = 70.76

SE = 0.53

tail $\bar{X}$ = 46.45

SE 0.86

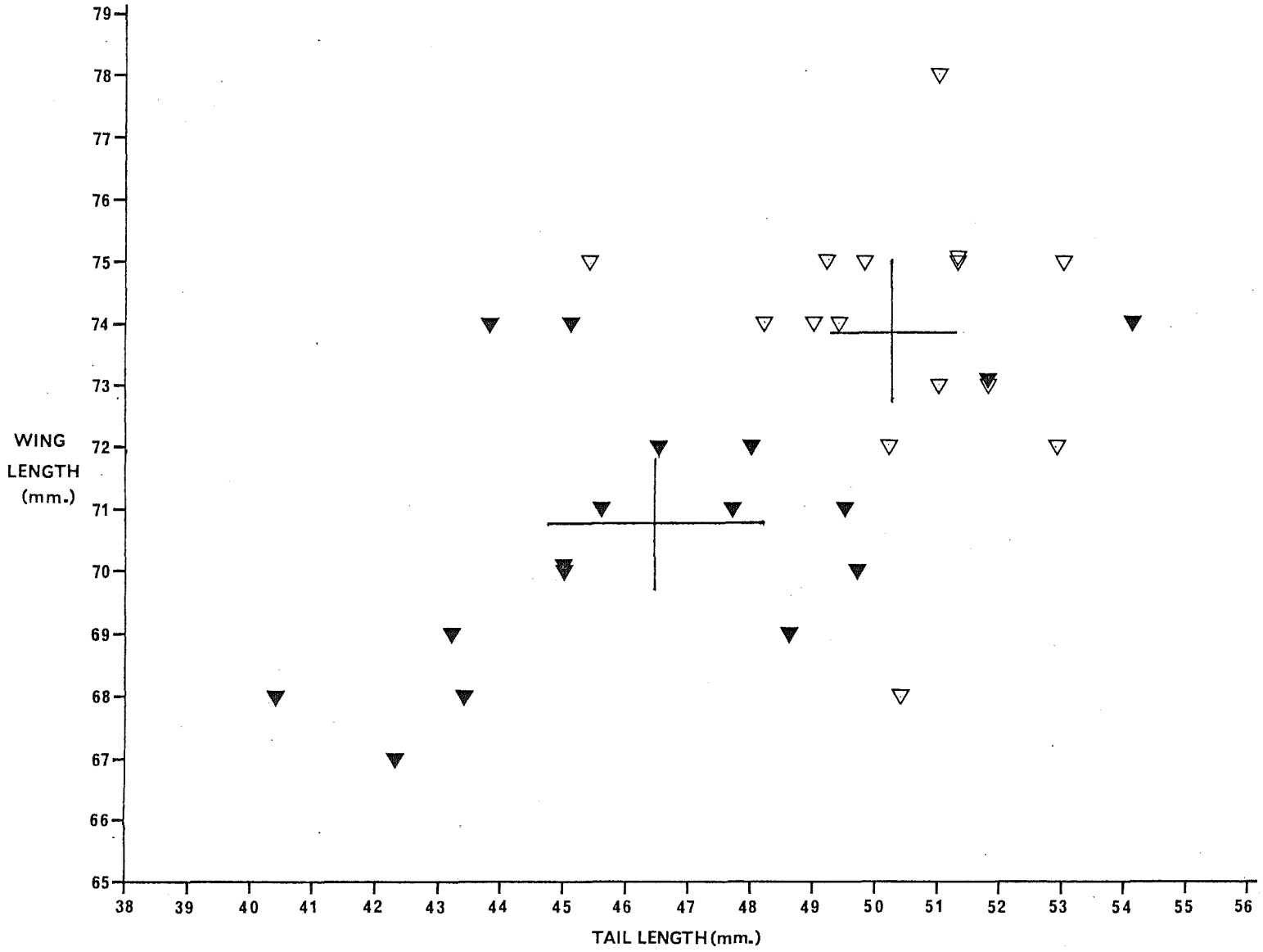
Male

wing $\bar{X}$ = 73.87

SE = 0.57

tail $\bar{X}$ = 50.26

SE = 0.50


WING
LENGTH
(mm.)
79
78
77
76
75
74
73
72
71
70
69
68
67
66
65
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
TAIL LENGTH (mm.)

While netting, individuals of a number of other species were captured. The results for these species are given in Appendix 3.

3.4 DISCUSSION

The sexes differed morphologically in two respects. Firstly, there were the colour differences between male and female plumages which allowed positive identification in the field, even from a distance. Secondly, the results from the captured birds revealed that males and females differed in three statistically significant ways, namely in the lengths of the tail and wing, and in total length. When the variables for wing length and tail length for each bird were plotted on a scattergram (Figure 3.1) the resulting spread of points showed a separation between the sexes, with the males having a higher mean value for the two variables than the females. A region of overlap occurred between the extreme values greater than the mean for the females and less than the mean for the males. The difference in total length between the sexes is accounted for by the different tail lengths. Fleming (1950) also found a significant difference between wing and tail lengths for the sexes, using measurements taken from museum skins.

Wing and tail lengths for birds in adult and juvenile plumage were combined because in the moult from juvenile to adult plumage the flight and tail feathers are not replaced (see Chapter 7). However, there will still be some variability in the measurements taken because over the course of a year, tail and flight feathers are subjected to wear and abrasion. Birds with newly moulted flight and tail feathers would probably give the most accurate measurements.

The frontal spot widths in adult and juvenile plumages for both sexes were significantly different. These were also visible differences. In males in adult plumage, the white spot contrasts markedly with the

surrounding black feathers, whereas the spot in males in juvenile plumage is difficult to see because it is small and heavily overladen with black-tipped feathers. Similarly in the females, the female in adult plumage has a white spot surrounded by brown feathers whereas the spot in females in juvenile plumage is visibly smaller and covered in brown-tipped feathers. Males and females in adult plumage had similar spot widths. The significance of the difference in spot depths between males and females in adult plumage was difficult to assess, because the birds can wax and wane their spot, thus affecting the depth. No differences for spot width or depth were found between juvenile male and female plumages.

The only major differences between nestlings and independent birds were the shorter wing and tail lengths in the nestlings. The short tail was also noticeable in newly fledged chicks.

In all birds the soles of the feet were orange, with the legs, iris and beak dark brown.

CHAPTER 4

TERRITORIAL BIOLOGY AND THE MOVEMENTS OF TITS

Territory: "any defended area" (Noble, 1939)

Territoriality: "one extreme of a continuum of responses of a bird to space" (Orians, 1971)

4.1 INTRODUCTION

The Yellow-breasted tit is a territorial bird maintaining a territory through aggressive behaviour (Potts, 1883; Buller, 1888; Philpott, 1919; Fleming, 1950; Poole, 1951). The length of time a territory is held, the intensity and duration of its defence, and the mechanisms involved in maintaining it, were poorly known before the present study.

Territoriality in the Pied tit is better known, particularly the role vocalizations and displays play in the maintenance of a territory (Bisset, 1978). General observations have also been made by M'Lean (1911) and Wilkinson and Wilkinson (1952).

Fleming (1950) summarized the territorial biology and movements of the five races of tits as follows:

> "This species is sedentary, undertaking few small-scale and no large-scale seasonal movements.... There is no gregariousness at any time of the year; pairs seem to remain together, in the general area of their nesting territories, all winter."

The investigation of territoriality and movements of Yellow-breasted tits of all ages in the study area throughout the year, formed a major part of the present study.

This chapter, after a brief discussion of the methods, is divided into four sections. Section A covers territory, territoriality and movements of birds, following the yearly cycle through in three parts: the prebreeding season (June to early September), breeding season (early September to February) and post-breeding season (February to June). Results are discussed for the two years studied, but only new trends or examples which reinforce patterns seen in the 1977 season are included for the 1978 season. Section B covers intraspecific relationships, examining the interactions between individuals. Section C discusses interspecific interactions. Section D is a concluding discussion, drawing together the results from the previous three sections and comparing them with other passerines to bring out differences and similarities.

4.2 METHODS

Whenever a known bird was observed, its position was noted with reference to the nearest landmark. Birds were recognized either from their band combination, occasionally by their song if they were males, or from being consistently seen in one area. Plumage differences were not sufficient to provide positive identification. All behaviour between, and of, individuals was noted.

To plot the position of a territory, all sightings of a bird were marked on a 14× enlargement of an aerial photograph of the study area, and the outermost points linked with a straight line. Points where the bird was observed outside its usual boundaries were not included. In calculating the area of a territory, allowance was made for the varying terrain within its boundaries. Corrections were made using either a 30^{o} or 40^{o} slope with all other areas being taken as flat. Triangulation was used to calculate the area so that the effects of the

terrain could be taken into account.

The 1977 prebreeding season was used as a period to familiarize myself with the behaviour of the birds, and mist netting techniques. Mist netting was restricted to the bush edge, and a small area of bush between stream HA and the south, south-east and north-east fences, (Figure 4.1) over this period. Only two birds were netted during June and July and none during August, but with the establishment of movement patterns seven birds were captured during September.

SECTION A

TERRITORY, TERRITORIALITY AND MOVEMENTS

4.3 1977 PREBREEDING SEASON

Behaviour during July and August

Territories located, and the capture points of birds banded during this period, are shown in Figure 4.1.

The majority of observations during June and July were made on unbanded birds in areas along the bush edge. Birds seen in the same areas on successive visits were classed as being on a territory, but because all males heard singing during this period sounded similar and were unbanded, individuals could not be recognized. Therefore, only an estimate of territory location, size and the number of birds present could be made. No details were gathered on birds resident away from the bush edge.

Tits were found to be absent from the part of the study area between stream HA and the south, south-east and north-east fences (Figure 4.1). Only a few call notes were heard near the bush edge. These may have been given by transient birds.

Figure 4.1

Territories are enclosed by the dotted lines.

Ⓐ streams

1 territory number

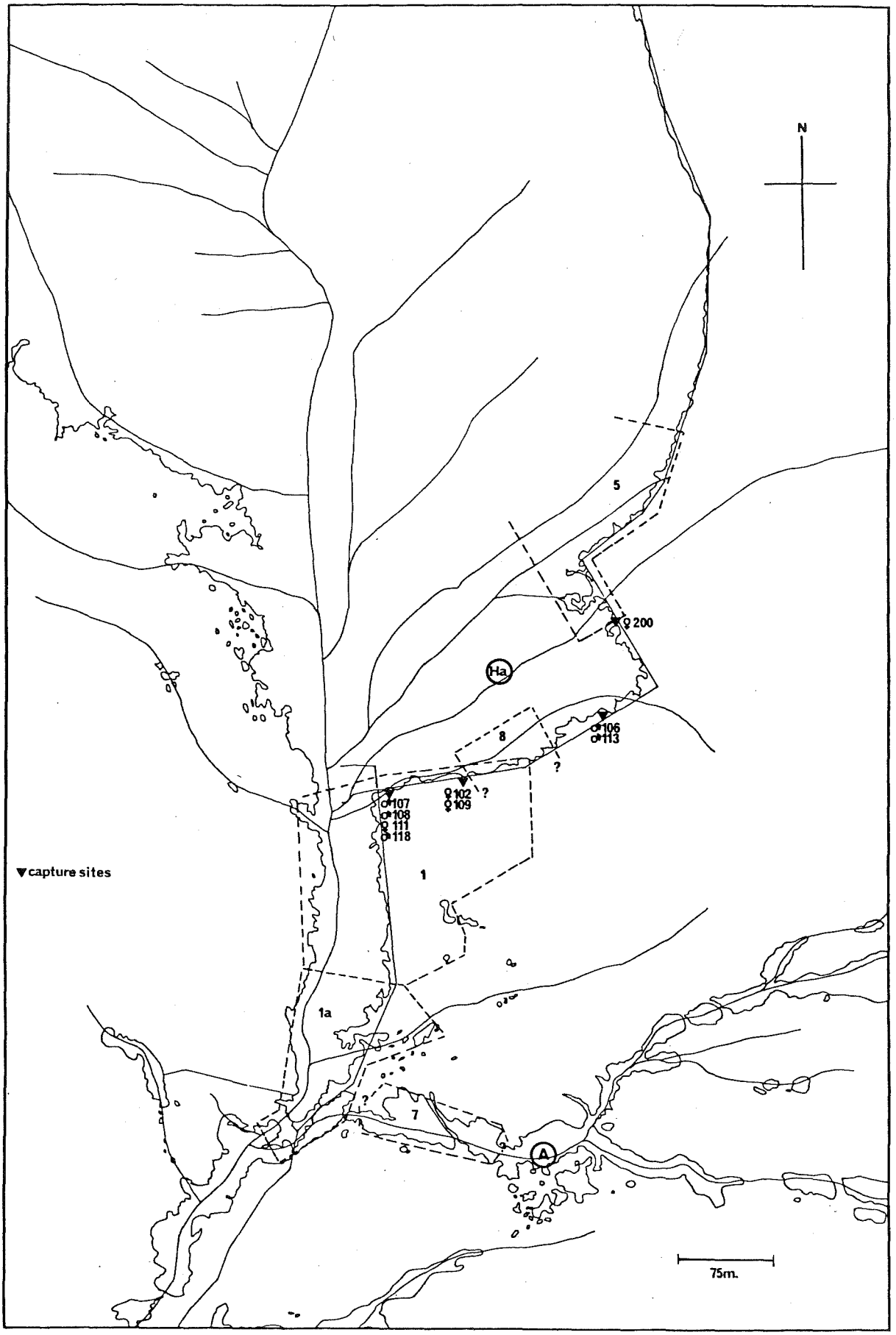


FIGURE 4.1 1977 Prebreeding season territories

During these two months, some birds inhabiting the bush edge were very obvious in that they moved out into the fields searching for food. Movement was restricted to areas in which suitable vantage points were available, from which to search for prey. These sites were varied and included rocks, logs and isolated trees and shrubs. Birds moved up to 100 m from the bush edge, but commonly moved about within 10 m of it. Only feeding took place during these excursions, and only individual birds, or one pair of birds, were ever seen in these areas. This suggested exclusive use by the tits resident in the adjacent bush. No defence of these areas was seen, however, and they appeared to be natural extensions to bush-edge territories.

Although pairs and individuals were on territories during July and August, some birds disappeared permanently, e.g. an unbanded pair of tits resident in territory 7 disappeared during August and was not replaced.

Distribution of birds and territories in late August and early September

By the beginning of September, birds were known to be present in four territories (1, 1a, 5, 8). No birds were present along the main stream below territory 1a, or along stream A where territory 7 had been occupied earlier in the season. The two females banded in June and July were not resighted over this period.

The recommencement of mist netting along the bush edge at the beginning of September produced immediate results. When male 106 was banded, it became apparent that he was residentin territory 1 and had been since at least the beginning of July. He was subsequently seen in the company of an unbanded female. This established that unbanded bachelor males were resident in territories 1a and 8.

Netting between 1st - 24th September revealed that there were

several birds along the top border of territory 1 which had previously remained undetected. Five birds were captured within the confines of territory 1. In addition, female 102 had been netted in this territory in June. Of these birds, only female 109, the mate of male 106, was resident in this territory. Male 106, however, was not even captured within his territorial limits. He was not seen outside these limits after his capture.

Around the borders of territory 1 therefore, five males were present - one below in territory 1a, and four along the top border. Male 118 was later found in the only territory abutting the top border of territory 1 during the breeding season. Female 111, captured twice in the same net over consecutive days, was not resighted after her last recapture, during the prebreeding season.

Therefore, two of the males banded (107, 108) and female 111 could not be accounted for as, apart from territory 8, no other territories were known to exist in this area. They had not revealed their presence before or after their capture, suggesting that they may not have been maintaining a territory, but were moving about quietly, keeping out of sight and hearing distance of resident birds.
Such birds are commonly termed floaters.

The only two banded birds seen regularly during the prebreeding season were male 106 and female 109, resident in territory 1. The further movements of birds banded over this period are discussed in section 4.4.

Behaviour of territory-holding birds

Throughout the prebreeding season the movement patterns of birds on territories remained the same. They were often seen on the bush edge searching for food and also commonly in the fields.

Although they were in supposedly exclusive territories, regular

trespassing into neighbouring territories occurred with little dispute resulting. Overlap between the males in territories 1 and 8 was seen frequently, but no fights or border disputes were seen. Therefore, although birds were on territories, borders did not appear to be well-defined. Sneaking about quietly when trespassing was probably more the rule than the exception.

During the prebreeding season, territory-holding males carried out two main activities: searching for food both in the bush and in the fields, usually in the company of their mates if they were not bachelors; and boundary patrolling and singing. By tracing the movements of a singing male defended borders could be defined, as countersinging sometimes occurred between neighbouring males. With regular singing between neighbours, the birds may come to recognize each other's song and thereby react less aggressively when they hear the other bird singing.

Males seldom sang near undefended borders (i.e. those which had no neighbours). Floaters were not observed searching for food in the fields.

Territory size and location

By the end of the prebreeding season the locations of four territories were known, all along the bush edge, but not all the inhabitants were identified. The area of three of the territories was calculated (Table 4.1).

Table 4.1 Territory size and occupation, 1977 prebreeding season

Territory	Male	Female	Area (hectares)
1	106	109	2.37 (incl. 1.04 ha of pasture)
1a	unbanded	-	1.00
5	*	*	1.38
8	unbanded	-	not calculated

- not present, * not identified.
Area for territory 5 is a minimum as not all boundaries were known.

4.4 1977 BREEDING SEASON

4.4.1 Adult birds

Territory shape and location for the 1977 breeding season is shown in Figure 4.2.

The sequence of events at the start of the breeding season.

The start of the breeding season was marked with the commencement of nest-building. The latter was not actually detected for the 1977 season but it probably coincided with the observed disappearance of females from the bush edge towards the middle of September. A drop in the feeding movements of both sexes into the surrounding fields also occurred at this time with the males rarely moving more than a few metres beyond the bush edge.

The population structure and territory setup did not remain stable over this period. Male 106, resident in territory 1, was last seen, with female 109, on 12-9-77, the day after she was banded. The bachelor males in territories 1a and 8 also vanished at that time, and an unbanded male appeared in territory 1. The latter was later seen moving about with female 109 in territories 1 and 1a, so that it is likely that he came from territory 1a.

Apart from the contraction of the territories to the bush edges, some pairs also abandoned areas of bush they had occupied during the prebreeding season. For example, the pair in territory 5 moved from the bush at the bottom border of their territory by stream Ha, up into the main body of their territory.

The fate of banded birds

Several banded birds were located, resident in territories away from the bush edge. This suggested two possibilities as to why banded birds were found away from the area of their original capture:

Figure 4.2

Territories are enclosed by dashed lines.

Numeral indicates territory number.

Ⓐ streams.

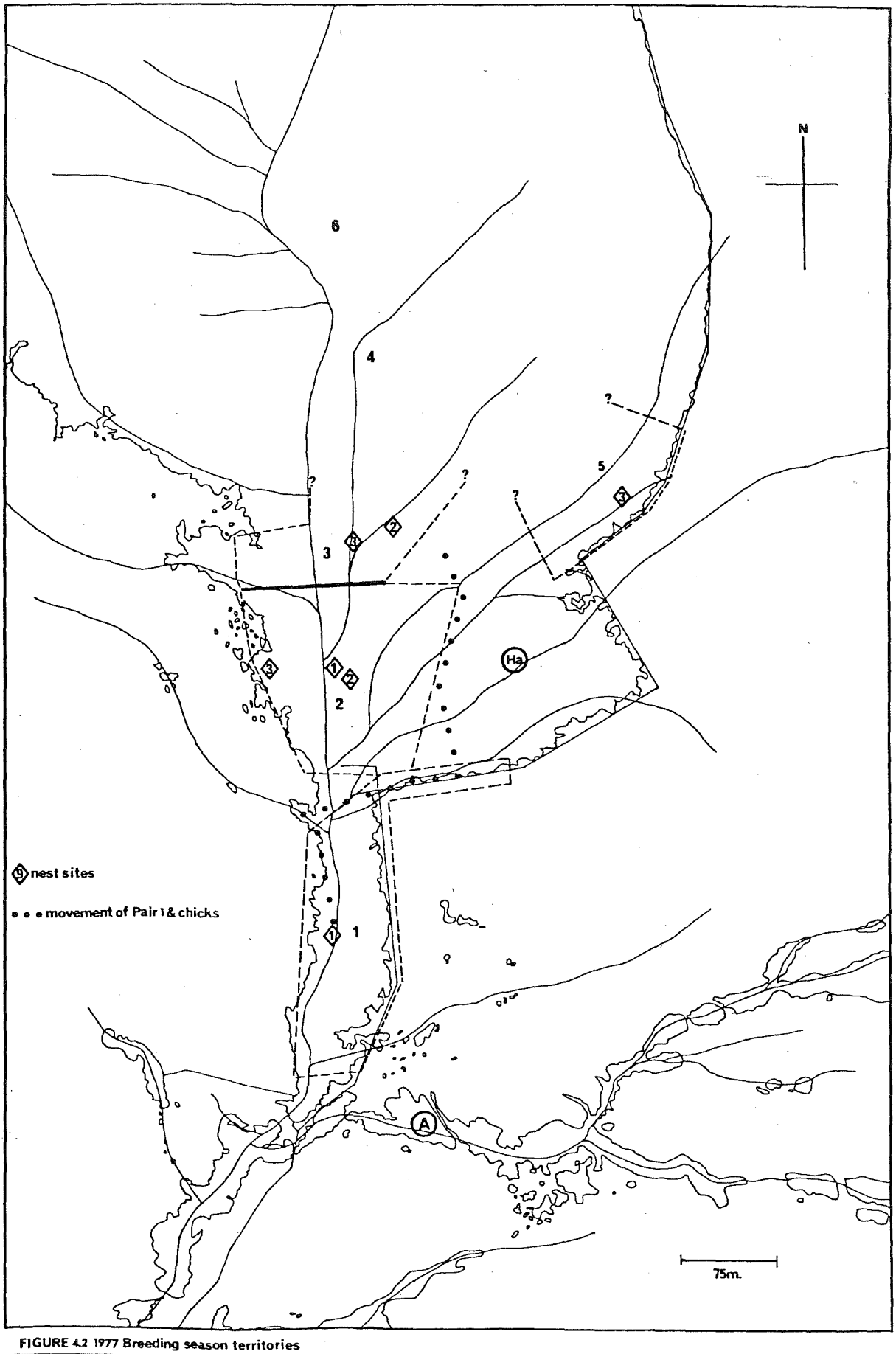


FIGURE 4.2 1977 Breeding season territories

1) During the prebreeding season there were a number of floaters present which did not remain in the area where they were captured. By moving about throughout the study area they eventually found a territory in which to settle.
2) Territory-holding birds made large-scale movements outside their territories during the prebreeding season and were captured as they moved about outside their normal boundaries.

Of the nine birds banded, before or at the start of the breeding season, males 107 and 108 were not seen again, and male 106 was replaced by an unbanded male in territory 1. Male 118 was resident in territory 2, and female 102, captured in June, was found breeding in territory 3. Female 200 and male 113 were resident in territory 5.

Female 111 appeared to be a floater. After her second recapture she was seen on the fence above territory 8 (Figure 4.1) on 3-10-77 and was resighted in territory 4 on 24-12-77. It was not established whether she bred in this territory, however.

Territory occupancy during the 1977 breeding season is shown in Table 4.2. In later discussion, the birds resident on a territory are referred to by their territory or band number, e.g. female 1, male 1, pair 1 or female 109, etc.

Table 4.2. Territory occupancy, 1977 breeding season.

Territory	Male	Female
1	unb.	109
2	118	unb.
3	unb.	102
4	unb.	111*
5	113	200
6	not identified	

* unsure of status, unb. = unbanded.

Territory location, maintenance and duration

Although territories were located deeper into the bush, the territorial boundaries could not be established in all cases (e.g. areas 4 and 6). No territories or birds were located between the east border of territory 2 and the north-east, south-east and south fences after the disappearance of male 8.

All territories located during the 1977 season included streams which ran continuously for the whole breeding season. Slope appeared to be of little importance, with both flat and steep areas being utilized.

Not all territories survived the breeding season. The pair in territory 1, after fledging their first brood early in November 1977, moved up the course of the main stream with their fledglings, passed through the eastern boundaries of their territory and carried on up the eastern border of territory 2. Seventeen days after the chicks had fledged, they all disappeared above the top border of territory 2 and were not seen again (their movements are indicated on Figure 4.2). The reason why they abandoned their territory is not known. Normally, the female rebuilds a few days after the chicks have fledged, but this did not occur on this occasion.

The three other territories, for which some of the boundaries were known, showed no shifts or border changes during the whole season. Male 2 did not extend his territory into territory 1 after the disappearance of pair 1.

Nest placement appeared to have no effect on territory boundaries. Nests were built away from defended borders but were not necessarily placed in the central area of the territory. For example, the 3rd nest of pair 2 was built about 3 m from the bush edge, whereas the other two nests were located in the central region of the territory. When a nest was built, however, the activities of the pair were centred about it

with the female moving a shorter distance from it than the male.

Defence of a part of the territory depended on the presence of a neighbouring bird. Boundaries which were shared with neighbours were patrolled more regularly than undefended boundaries. Of the four territories plotted, two had two neighbours and two had one neighbour. As a result, accurate territorial limits could not be plotted for some territories because males only sang along their defended border. The males were commonly found along these borders, often countersinging with their neighbours, when they were away from the nest site. Border disputes, however, were rare.

Some defended borders were patrolled more regularly than others. For example, male 2 originally shared borders with males 1 and 3, but was seldom observed near his border with male 1. Instead, he spent nearly all his time patrolling the border shared with male 3, or searching for food along it. Male 5 shared his top border with an unidentified male. However, very little territorial activity was seen in this area. Regular border patrolling may take place only if the neighbouring male sings in the area.

The main form of territorial activity employed to maintain boundaries, therefore, was singing. If the neighbouring male was nearby, then countersinging often took place. Border disputes involving displays and fights were rare, possibly because of the low number of neighbours and hence low territorial pressure.

Movements of territory-holding birds

Territory-holding birds, for the most part, stayed on their territories throughout the breeding season. Occasionally, however, the males moved beyond their boundaries into unoccupied areas. These movements were associated with feeding, and few or no vocalizations were given. Challenges took place, however, if, in their movements, they

strayed on to another territory. In one example, male 5 was feeding from the south-east fence at the eastern border of territory 1. He was seen by male 1 and successfully challenged and driven off.

Deliberate trespassing into neighbouring territories also occurred. If the trespassing bird remained silent, he moved about freely in the border areas of his neighbour's territory without the owner knowing. Trespassing also occurred when a suitable bathing site was available in another territory. In one case, male 3 was seen bathing in a stream in male 2's territory near pair 2's first nest site. pair 2 also bathed in the same spot.

When moving about with dependent fledglings, a pair usually remained within their territorial boundaries or moved about in unclaimed areas, but when trespassing into neighbouring territories did take place the owners did not challenge the trespassers.

Females were not observed trespassing into neighbouring territories, probably because they did not move as far from the nest site as the males.

Territory size

Territories remained stable in size after the initial contractions at the start of the breeding season. Table 4.3 gives territory sizes and the size of changes from the prebreeding season. Territory size varied considerably and may have been influenced by the number of neighbours a bird had.

Table 4.3 Territory size, 1977 breeding season.

Territory	Area (ha)	Size of contraction (ha)
1	1.66	1.32
2	2.05	-
3	1.54*	-
5	1.17*	0.69

* minimum size, not all boundaries known.
- not measured.

4.4.2 Independent juveniles and immatures

Territories and birds discussed in this section are detailed on Figure 4.3.

There was no natural break between the end of the breeding season and the start of the post-breeding season for juvenile and immature tits. This section covers both periods for these birds.

Activities of newly independent juveniles.

Breeding activities commenced within a short span of time for all pairs of tits in the study area (see Chapter 6), with independent juveniles from successful first nests appearing during late November and early December. They remained in and about their parental territories for several weeks after independence, continually moving about, and searching for food.

For about the first week after independence some juveniles moved about in pairs. Two females, or a male and a female, were more commonly seen than two males, as young males usually chased each other on meeting. After this period all juveniles moved about individually, seldom approaching other tits. The call notes given by these birds may have assisted them in avoiding each other.

However, as they moved about, interactions withother tits did occur. Adult males reacted more aggressively to the presence of juveniles than did adult females, and displayed a stronger reaction towards juvenile males than to females. The commonest interactions seen were chases with more aggressive behaviour seen only rarely (see section B). Occasionally, adult birds ignored the juveniles. When two juveniles met, a chase often resulted.

When the adult birds renested they centred their activities about their new nest site, remaining in this area until the next brood fledged.

Figure 4.3

Territories are enclosed by dashed lines, and identified by letters or numbers.

Ⓒ stream.

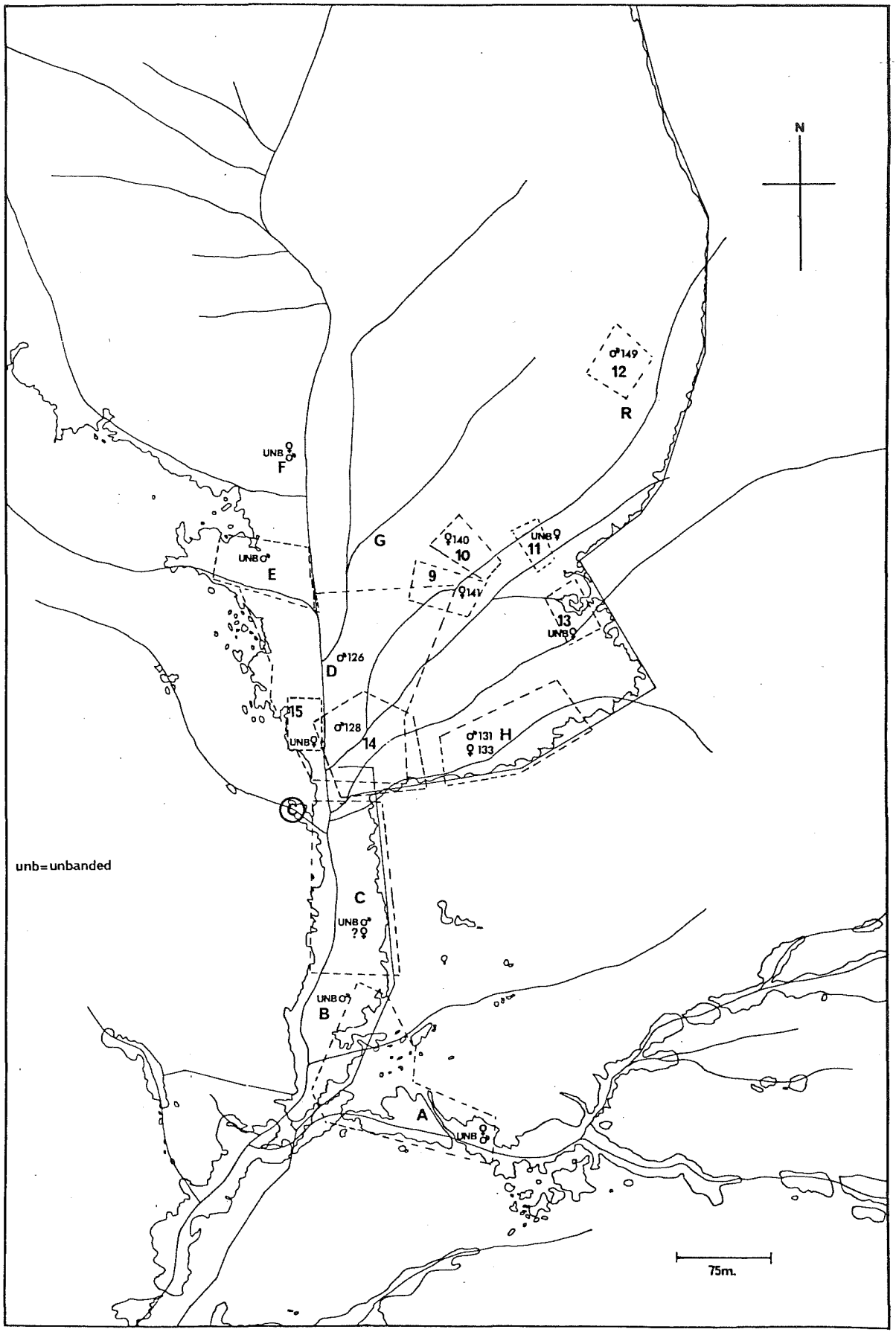


FIGURE 4.3 Juvenile–immature territories, January to late March 1978

Juvenile tits which moved about this centre of activity usually gave few vocalizations, possibly to avoid confrontation with the adult male who chased even silent juveniles. This can be contrasted with juveniles inhabiting the peripheries of a territory, or undefended borders. These birds were much more vocal and hence more conspicuous, probably because these areas were seldom visited by the male. The resident adult male, however, retained dominance over his entire territory, chasing off juveniles when he saw them.

Because no juveniles were banded until late January, the movements of individual birds could not be followed for any longer than a few hours at a time. In some areas, juveniles were seen on nearly every visit to the study area, suggesting that some birds may have been resident in one area.

Dispersal

Independent juveniles seen up to mid-January 1978 were from first broods, because juveniles from the second broods could not reach independence before then. This allowed their territorial behaviour and movements away from adult territories to be followed, but because they were not banded their parental territories could not be established.

The dispersal of some juveniles from established or parental territories did not occur through random movement. Instead they appeared in areas where they had not been seen previously, over a short space of time. Estimation of the timing of dispersal and whether a synchronized movement was involved was determined by noting when juveniles appeared in unoccupied parts of the study area.

Several parts of the study area were not occupied by adult tits for the duration of the 1977 breeding season. With the disappearance of pair 1, no tits were resident below territory 2 from mid-November onwards. The area between the east border of territory 2 and the

north-east, south-east and south fences was also unoccupied from mid-September onwards (Figure 4.2). No juvenile tits were seen in these areas until the first week in January, five to six weeks after they became independent.

The first date on which juveniles were seen or heard below territory 2 was on 4-1-78 when a male was seen and heard singing juvenile song near male 2's bottom border. After this date, call notes were heard and juvenile tits were regularly sighted in abandoned territory 1. By 8-1-78 a male, possibly in the company of another tit, was seen along stream A and on 21-1-78 birds were seen flying between stream A and the main stream. Below this area, call notes were heard as far down as the area adjacent to the shearing shed (see Figure 2.4) over the following two weeks.

In the area to the east of the east border of territory 2, a female and possibly a male were seen near the south-east fence on 6-1-78. Call notes were heard throughout the area after this date. Similar patterns were observed in other parts of the study area where no adult birds were resident. If these birds had appeared in the unoccupied areas through random movement, then regular sightings of juveniles from independence onwards might have been expected in such areas. Occupation of these areas through randon movement would have been assisted by the fact that the pairs in the territories which bordered on at least one of these areas (territories 2, 3 and 5), all raised juveniles to independence.

Territorial activities.

After about two weeks of independence some males and females set up small subterritories within, or along, the boundaries of adult territories. The remaining birds continued to move about throughout the area. These subterritories were sometimes maintained for no more than

two to three weeks, after which time the resident birds disappeared.

Birds which dispersed to vacant areas after five to six weeks of independence set up territories in these areas and excluded other tits from them. Juveniles which did not disperse continued to move about in the adult territories or remained on subterritories. The boundaries of both types of territory were advertised with loud call notes and juvenile song (see Chapter 9), and defended by chasing intruders away.

Comparison of territories in vacant areas with those on the outskirts of adult territories showed that those in vacant areas were larger and were in existence for a longer period of time. Intruding juveniles were seldom seen in these areas, suggesting that only a small proportion of juveniles were involved in the dispersal.

By the time the second broods became independent in mid-January many older juveniles had well-established territories which they defended against other tits. Therefore, newly independent juveniles had to avoid both adult and older juveniles. A similar situation would exist for birds becoming independent after this date also.

Results of banding.

Mist netting recommenced from the end of January 1978, so that the duration of territories, territorial behaviour, and the movements of known birds could be monitored. This section deals with the results from banded, and known unbanded birds.

Territories were of variable shape and size, and were maintained for a minimum period of about two weeks. However, juvenile territories were not always exclusive areas, as overlaps between adult and juvenile, and between juvenile territories, occurred. Trespassing took place while the resident bird was in another part of its territory or when it did not advertise its presence.

The following examples illustrate the variability in territory duration, size and overlap. All territories discussed are shown in Figure 4.3. Additional territory localities are also shown.

1) Male 128, banded on 30-1-78, was resident in territory 14 from 4-1-78. His territory overlapped completely with the bottom part of territory 2 and he was observed in this area until 7-3-78 when he disappeared.
2) Male 126, banded on 29-1-78, was observed from this date onwards moving throughout territory D. This territory occupied the same boundaries as territory 2 and was the largest known juvenile territory. It overlapped with territories 9, 14 and 15. The male regularly chased other juveniles on meeting them.
3) Female 140, resident in territory 10, was captured on 15-2-78 and resighted in the same area on 7-3-78. She was not seen after this date.
4) A pair of juveniles were present in territory C from the third week in January, the female being banded but not identified. The area these birds occupied was similar to that of territory 1 before the 1977 breeding season. There was little or no overlap with other territories.
5) A pair of juveniles, both banded on 30-1-78, were resident in territory H from early January onwards. These were the only two birds ever seen in or around this territory.

Other banded and unbanded tits were not on territories. They moved about continually and were rarely observed.

In other cases, birds were banded and were then presumed to have shifted from the area as they were not resighted in the following days. Then, at a later date, they were resighted or recaptured in the same area. This meant that they were resident in the area, remaining

inconspicuous and not advertising their presence with vocalizations. For example, female 141 captured on 15-2-78 in territory 9 was not seen again until her recapture in the same area on 1-4-78. She was not resighted after this date.

During late January and early February when adult breeding activities were completed or nearing completion, four or five juveniles could sometimes be found within a restricted area in a small part of an adult territory. They moved about individually and avoided each other but did not display the usual territorial behaviour involving aggressive interactions and vocalizations.

March to late May

By March 1978 all breeding activities had been completed (see Chapter 6), and the adult birds had ceased to defend their territories and had retired to moult. This allowed juveniles, many of which were also moulting over this period, to establish and maintain territories in the undefended adult territories.

Birds which had set up territories in formerly vacant areas, during January and February, continued to maintain and defend them against intruders. However, these birds did not remain on their territories all the time as occasional excursions were made into other territories. For example, the banded pair in territory H was observed by stream C on 21-3-78, but both birds were seen back in their own territory a few days later. Regular trespassing by other birds also occurred.

Between March and late May, juvenile subterritories that had been set up on the peripheries of adult territories ceased to exist. Some of the former residents were never seen again, and others were resighted in different parts of the study area, i.e. dispersal was still taking place. No clear pattern of movement was evident because birds which became independent at different times of the

breeding season were probably involved. Juveniles from second and later broods may have shown the same synchronous movement away from adult territories, as seen in some first brood birds. The movements of some birds banded in late-January and early-February are shown in Figure 4.4. The following examples illustrate this delayed movement.

1) Male 125 was banded on 29-1-78 in adult territory 3. There were several probable resightings in the same area during February and March, but on 7-4-78 he was resighted along the bottom border of territory D. He was not seen again.
2) Male 128, resident in territory 14, was not observed in his territory after 7-3-78. He was resighted on 21-3-78 near stream A but was not seen again after this date.
3) Male 149, banded on 10-3-78, was recaptured on 18-3-78 in territory 5 but was not seen after this date.

From April onwards, the number of immatures resident in the study area began to drop. Birds resident in well-established territories in formerly vacant areas remained in these areas. The main casualties appeared to be those birds resident in subterritories on the peripheries of adult territories, and birds which had not established territories (i.e. floaters). The fate of these birds was not determined, although some may have left the area voluntarily while others may have been driven out by adult birds reclaiming their territories after the completion of their moult in late April.

No territories had been established below stream A, and some areas which had been vacant during the early breeding season, but later occupied by juveniles, had become vacant again.

By the end of May the numbers of tits present in the study area appeared to have stabilized; some territories had been occupied for several months, and pair-bonds were well-established.

Figure 4.4

Ⓐ Stream.

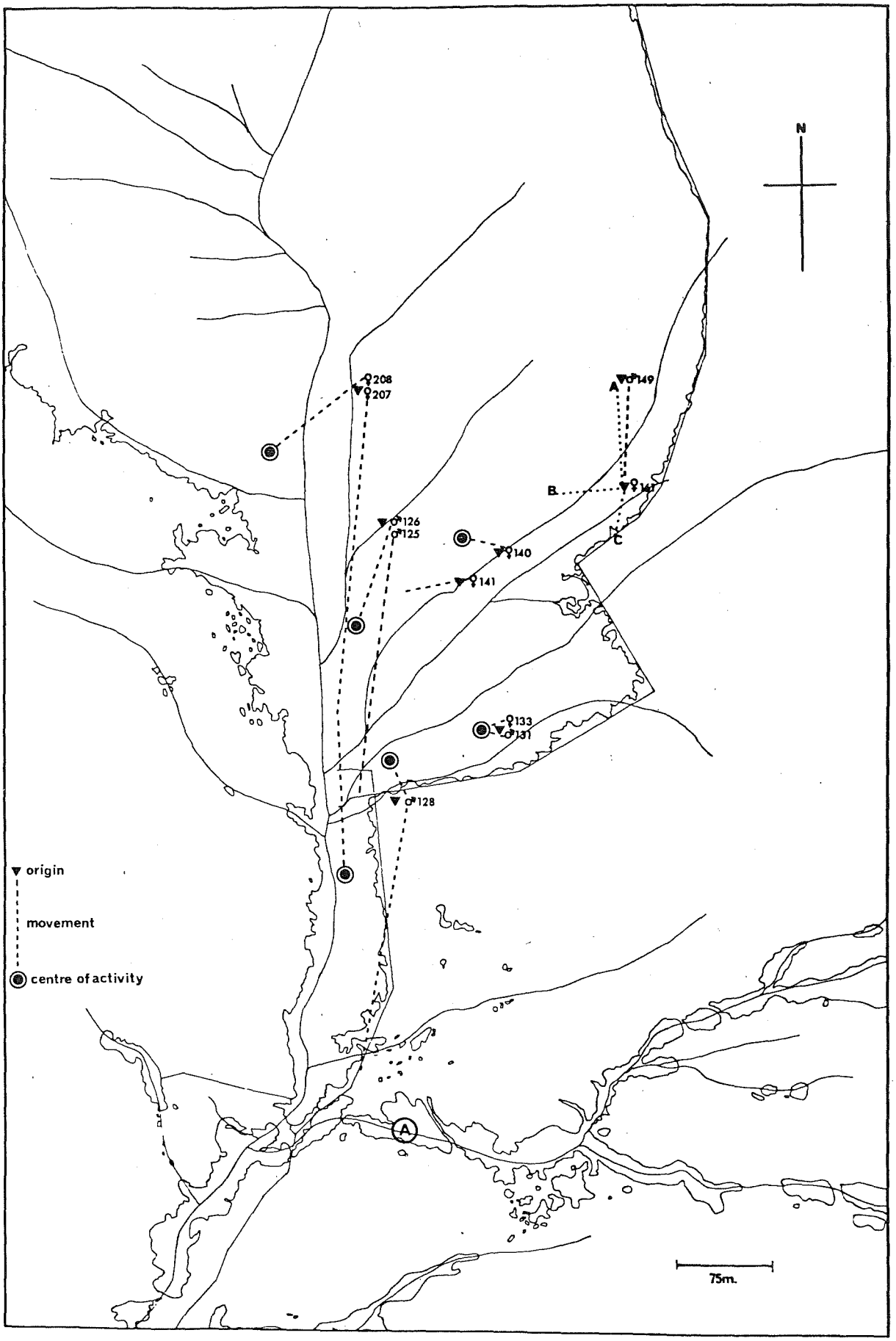


FIGURE 4.4 Origin and movements of banded birds prior to and for the 1978-1979 breeding season

Territory boundaries, however, were ill-defined with no boundary patrolling apparent or song being heard. There were still a number of floaters present, as individual birds were sometimes seen moving through occupied territories. Tits also appeared to tolerate other tits near them, showing no aggressive reactions. For example, the behaviour of female 161 can be used to illustrate the movements of a floater and the tolerance shown towards other tits. She was banded on 18-3-78, but was not resighted until 28-5-78 in area A, above her capture site (Figure 4.4). The next day she was seen in area B within a few metres of two other females, all of which were in clear view of each other. They ignored one another and eventually moved apart. Female 161 was later seen in area C on the same day but was never seen again after this date.

4.5 1977 ADULT POST-BREEDING SEASON

Breeding activities concluded between mid-January and late February with the independence of the last broods. The adults withdrew to a small part of their territory and moulted. They gave few vocalizations, and the males did not react to a taped song played in their territories.

Because of their secretiveness over this period, their activities could not be followed. During the post-breeding season, no adults were seen after late April.

This behaviour can be contrasted with that of the juvenile and immature birds, many of whom remained conspicuous and very vocal throughout the whole period, even while they were moulting.

4.6 1978 PREBREEDING SEASON

Territories located during this period are shown on Figure 4.5.

Figure 4.5

Territories are enclosed by dashed lines.

The capital letters identify individual territories.

The heavy black lines indicate rigidly defined boundaries.

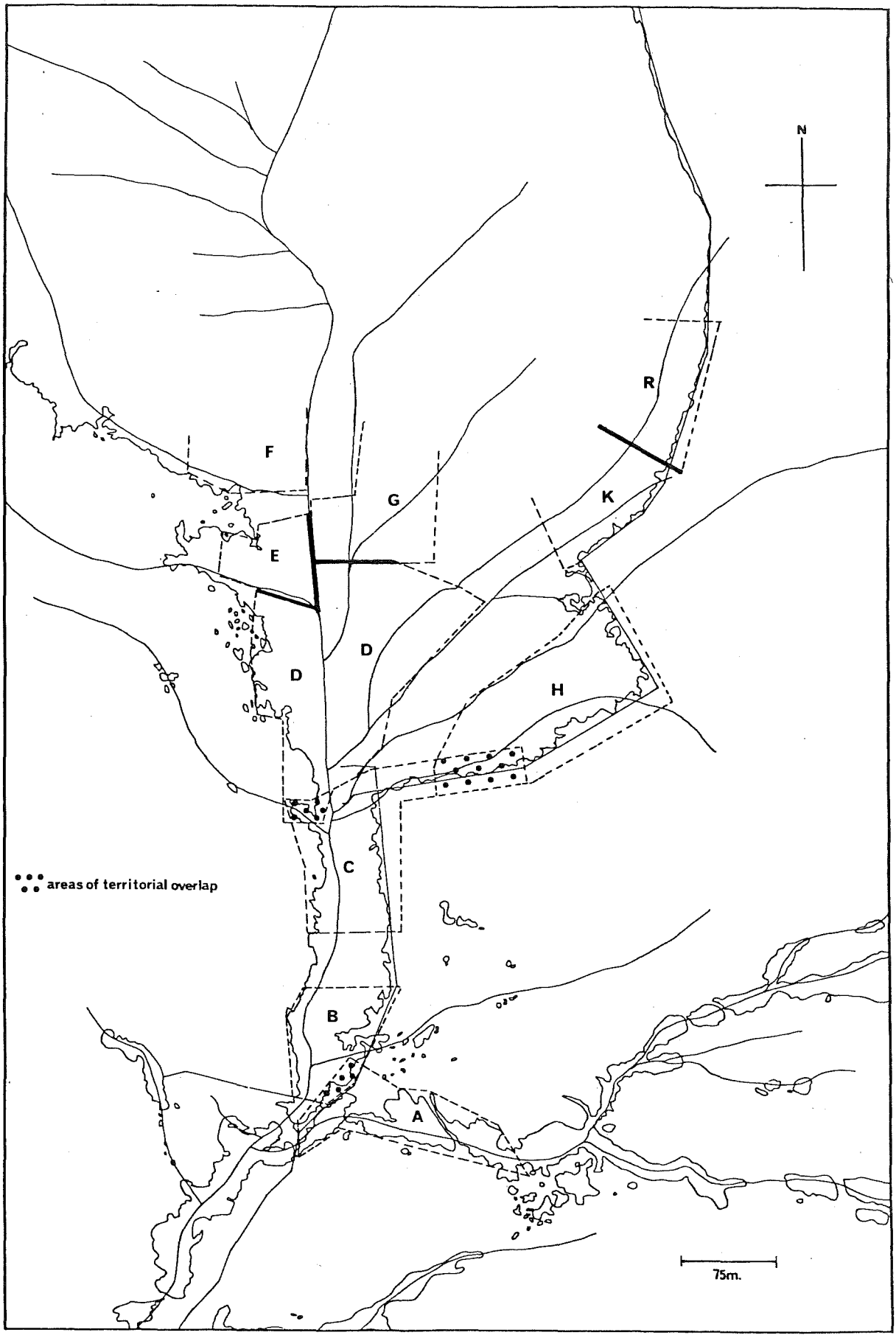


FIGURE 4.5 1978 Prebreeding season territories

June

During June, established territories remained intact, but with ill-defined boundaries. The pair-bond remained strong, with the birds moving about together searching for food. No feeding of the female by the male was seen.

Members of two well-established pairs disappeared late in June. In one case, male 131 resident in territory H disappeared and was replaced by an unbanded male. The resident female moved about with the new male. In the other case, the unidentified banded female in territory C was replaced by female 207 who had been banded in territory 4 (see Figure 4.4). (Female 207 had been banded after the original banded female had appeared in territory C.) This suggests that female 207 may have been a floater and had moved about the study area until she found a territory without a female. Few non-territorial birds (i.e. floaters) were seen after the end of June.

Over this period the distribution of tits in the study area became patchy as they confined their activities to small parts of their territories. This was probably caused by the distribution of the fuchsias, as they lost their leaves over the winter and probably affected the food supply. Activities were confined to the areas with thicker and more permanent leaf-cover.

July to early September

By July, the tits inhabiting territories bordering on the bush edge were seen moving about in the fields searching for food. This was the same situation existing for the corresponding period during the 1977 prebreeding season. Behaviour was also similar for the two periods, i.e. no territorial advertising or boundary disputes.

No floaters were known to be present in the study area below territories D and H, although one unexplained sighting was made on

6-8-78 when a pair of tits moved up the east boundary of territory G, eventually disappearing. This pair was not seen again and may have had a territory located elsewhere.

The layout of territories was better known for the 1978 prebreeding season than for the 1977 season, and by mid-August the whereabouts of 10 territories was known. Their locations remained the same until the start of the breeding season.

The large amount of overlap between some territories became evident during August when males, in particular, began moving throughout their territories, sometimes singing. Song became more frequent as the breeding season approached so that the movements of males were easily traced. Despite the overlaps, no boundary conflicts were seen during the prebreeding season. Instead, the commonest form of territorial maintenance was singing while boundary patrolling, but when trespassing occurred the birds usually remained silent. In the region of overlap between pairs C and H, pair C usually trespassed into territory H when pair H was near their north-east border. Male C was heard singing in this area as late as 7-9-78 but he was not challenged by male H.

Males C and D regularly sang throughout the area of overlap between their territories, but no other territorial activity apart from song was used.

Rigidly defined borders existed between some territories, however. For example, regular countersinging was heard along the borders between males D and E, E and G, and D and G. No trespassing occurred.

Although females may have been with the males while they were countersinging, they took no part in the maintenance of boundaries.

Therefore, the main activities of the males during the late prebreeding season were moving throughout their territories singing, countersinging along rigidly defined borders, and trespassing regularly across other less rigidly defined borders. The intensity of the reply

from the neighbouring males may have determined the amount of trespassing which took place.

Territory area.

All known territories contained at least one major stream and again were located in all types of terrain.

Movements into the fields by birds resident in bush edge territories were less obvious during the 1978 breeding season when compared with the 1977 season. This may have reflected the available food supply in the bush.

Table 4.4 lists the areas for known territories near the end of the 1978 prebreeding season.

Table 4.4. Territory area at the end of the 1978 prebreeding season.

Territory	Area (ha)
A	0.64
B	0.63
C	1.24
D	2.22
E	0.58
F	1.40*
G	0.85*
H	1.33
K	0.72*
R	0.76*

* minimum area, as not all boundaries were known.

4.7 1978 BREEDING SEASON

4.7.1 Adult birds

Figure 4.6 shows the location of territories and nest sites during the 1978 breeding season.

Figure 4.6

Territories are enclosed by the dashed lines.

Territories are identified by the capital letters.

The thick black lines indicate the presence of

rigidly defined borders.

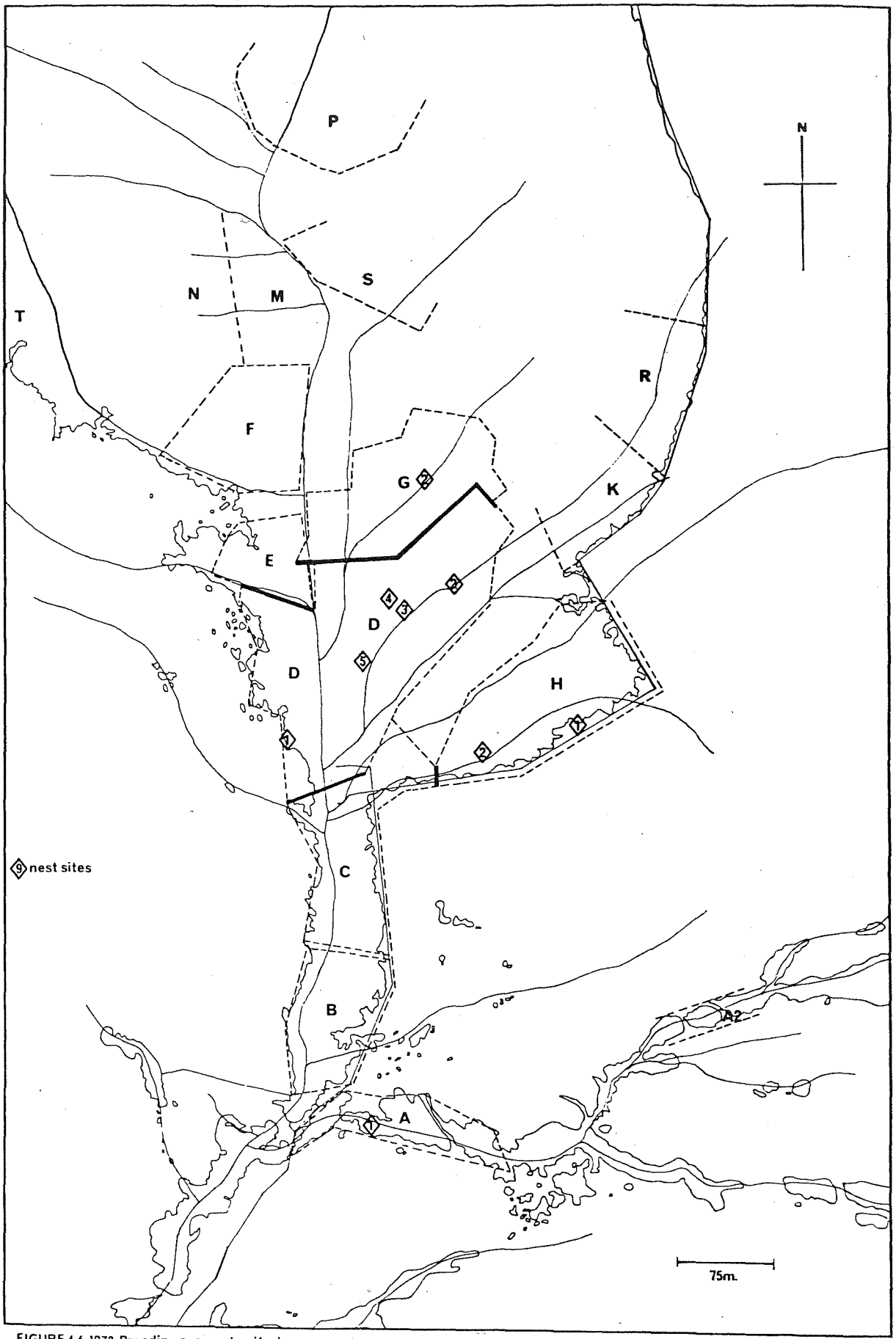


FIGURE 4.6 1978 Breeding season territories

By the start of the 1978 breeding season, the boundaries between neighbouring territories were well-defined, with no overlaps or trespassing occurring. Where overlaps had formerly occurred, vigorous countersinging was heard.

As in the 1977 season, the cessation of movement out into the fields by birds in bush edge territories signified that breeding activities had commenced. The earliest date on which nest-building was seen was 7-9-78.

Pair-bonds remained stable throughout the breeding season, with no known partner replacements observed.

Territory occupancy.

A) 1977 Adult birds

Of the six banded birds breeding during the 1977 season, only two were known to have survived to the 1978 season. These were female 111, now resident in territory G after being sighted in territory 4 (Figure 4.2) during the 1977 season and recaptured in territory G on 6-4-78, and female 200, resident in the same territory as the previous year but with a new male.

In addition, the unbanded male in territory G may have been the same male that was present in territory 3 in 1977. Sonagraphic analysis of the songs proved inconclusive (see Chapter 9).

B) Birds bred during the 1977 breeding season

Some birds fledged during the 1977 breeding season had been resident on their territories since the first outward movement in January 1978. (Two of the birds which had disappeared over the winter had also been resident in the same territory from about mid-January onwards.)

This suggests that birds fledged from the first broods of the season may have an advantage over birds from succeeding broods, as they gained access to vacant parts of the study area first and were able to

set-up and maintain territories. Birds fledged later in the season may have had to move about more, waiting until they could usurp an owner or replace a lost mate. In turn, this may have affected the survival rate of birds from later broods, or perhaps forcing them to leave the area.

The following examples illustrate the length of time some territories had been occupied:

1) A pair of unbanded birds had been resident in territory A since late January.
2) An unbanded bachelor male was present in territory B from early May onwards.
3) A pair had been present in territory C from mid-January onwards, but the female disappeared in late June and was replaced by female 207.
4) Male 126 was seen moving throughout territory D from mid-February onwards. Male 118, resident in this territory (= territory 2) during the 1977 breeding season, was last seen in late April 1978. Male 126 appeared to have taken over the territory completely by this time. A dispute between these two males was never observed. The female with male D was unbanded.
5) Male E, an unbanded bachelor male, had maintained a territory since early February. He was recognized through his behaviour as he always moved about within the same restricted area.
6) Territory F had a number of ownership changes. An unidentified banded male was seen in this territory in March, but later disappeared. By September an unbanded male was resident along with female 208 who had been banded in the area in April.
7) Female 133 was resident in territory H from early January onwards with male 131. After his disappearance in late June, an unbanded male took over the territory.

8) Female 200, which bred in the 1977 season, lost her original mate during the post-breeding season. A male was not identified in this territory until an unbanded male recognizable through his very distinctive song (see Chapter 9) began singing in early August.

Despite there being new resident birds, particularly males, in most of the territories, a comparison between the location and shape of the 1977 and 1978 territories revealed remarkable similarities (Figures 4.2 and 4.6). Territories B, C, D, G and K were in similar locations to territories 1a, 1, 2, 3 and 5 respectively, with some boundaries being in exactly the same positions. Territory 3, however, had been divided between males E and G. Territories A and H were not occupied during the 1977 breeding season.

Of the 18 tits banded during and after the 1977 breeding season, only four were known to have survived to breed in the 1978 season. In addition, two further banded birds disappeared during the prebreeding season. Other banded birds may have been resident outside the study area or left the area.

Table 4.5 lists the residents of territories during the 1978 breeding season.

Table 4.5. Territory occupants during the 1978 breeding season.

Territory	Male	Female	Territory	Male	Female
A	unb.	unb.	H	unb.	133
B	unb.	-	K	unb.	200
C	unb.	207	M	*	unb.
D	126	unb.	N	unb.	*
E	unb.	-	P	unb.	*
F	unb.	208	R	*	unb.
G	unb.	111	S	unb.	*

\- not present
* not identified
unb. = unbanded.

Territory survival.

As in 1977, not all territories survived the breeding season. The pair in territory A disappeared during the construction of their first nest, early in September. The female was relocated further upstream in early November (area A2 on Figure 4.6). It is not known whether this pair bred successfully. Male B, a bachelor, disappeared from his territory during October.

The pair in territory C exhibited a similar behaviour pattern to the pair in the same territory in 1977. They disappeared early in November, at about the time their nestlings should have fledged. Male E, a bachelor, may have shifted to another, less accessible part of his territory.

The nest site was the focal point of adult activities. Only one territory changed shape markedly during the 1978 season and this was due to the placement of successive nests by the female. Boundary extensions occurred for the 2nd, 3rd and 4th nests of pair D (and also demonstrated that nests were not necessarily placed within the central part of a territory). Figure 4.7 shows the successive changes in the top boundary of territory D with the changes in nest site. The first nest was built about two metres from the bush edge (Figure 4.7a). The boundaries remained the same as they had been before the start of the breeding season. After the loss of this nest to a predator, the second nest was built in a totara on the top boundary of this territory, which was undefended (Figure 4.7b). (Male C was seen at pair D's first nest site within a day of it being abandoned. He probably trespassed up this far because male D no longer sang in the area.)

Male D then started singing above the new nest site, spending most of his time in this area. Male G also began singing in the area and eventually a border was established (Figure 4.7b). Regular counter-singing and calling continued to be heard along their original shared

Figure 4.7

Boundary changes with successive nests - pair D.

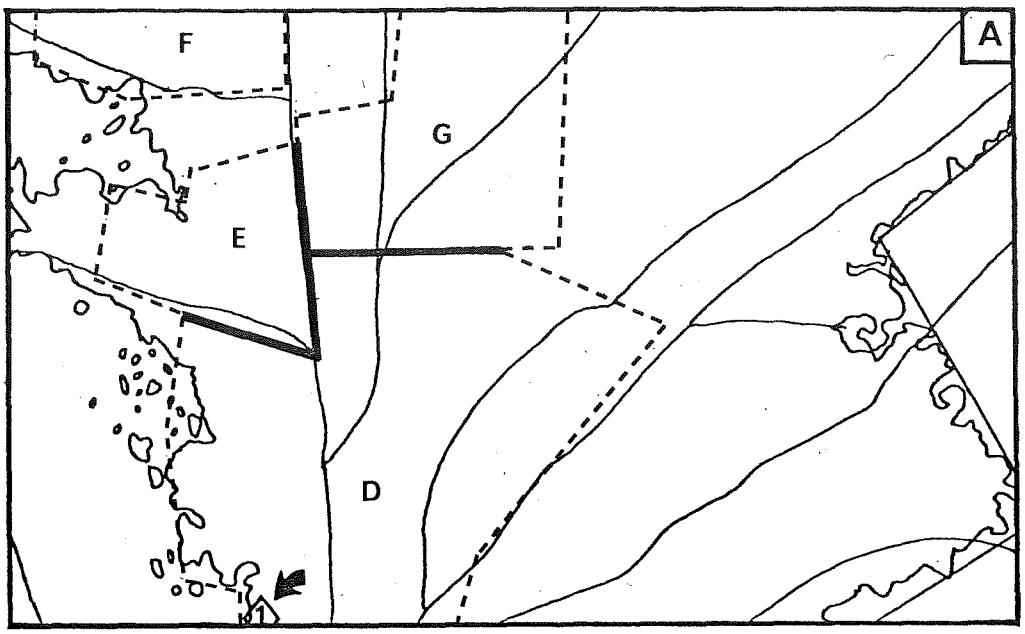
A. Boundary location - nest 1 (1st nest arrowed).

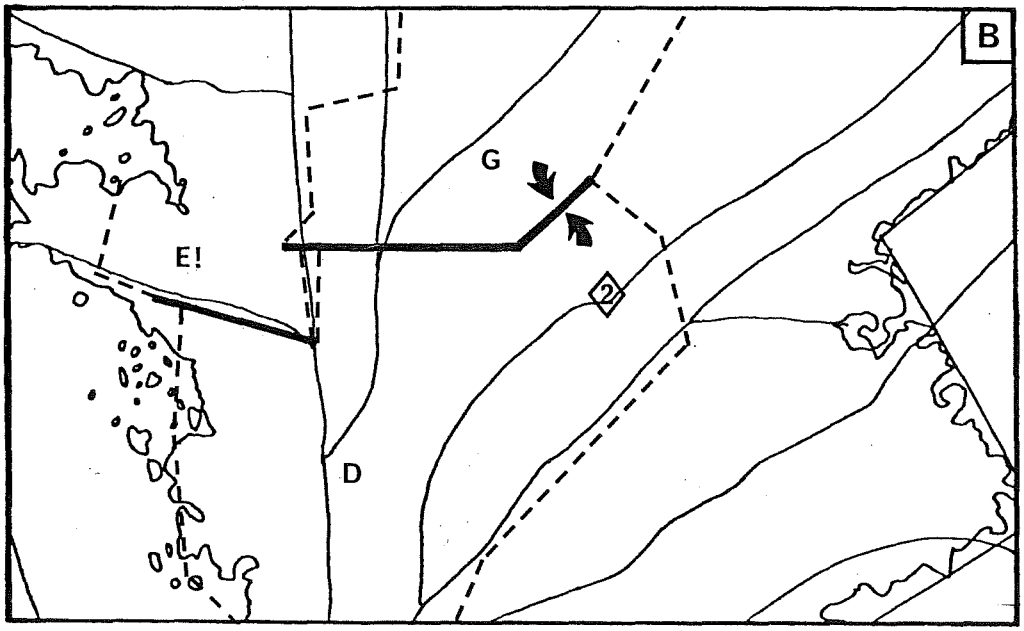
B. Boundary location after the building of the 2nd nest - new boundary is arrowed.

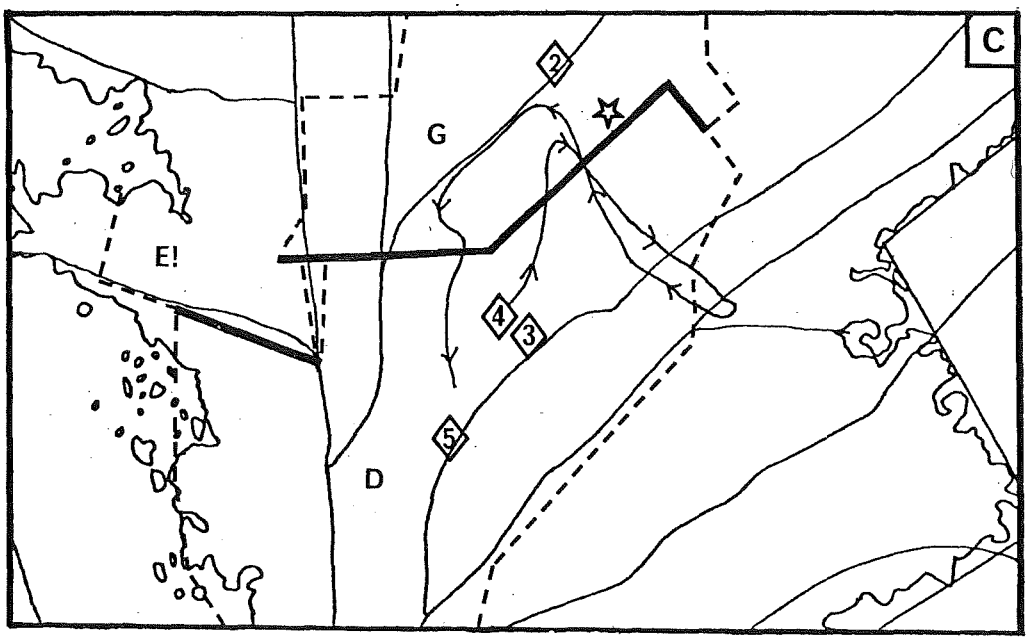
C. Boundary location for 3rd and 4th nests.
Site of conflict is starred.
The path taken by male D and his fledglings is shown by the arrowed line.

Successive nests are indicated by the number within the diamond.

Scale: 1 cm = 28 m (approx.).


A
F
G
E
D
1


B
G
E!
2
D


C
2
G
E!
4
3
5
D

boundary. With the abandonment of the second nest and the construction of the third, male D continued to expand his territory into the vacant areas above the nest site. While he was moving about singing he trespassed into male G's territory. This resulted in a full-scale border dispute about 20 m from pair G's second nest site (Figure 4.7c). Eventually a boundary was established which was regularly patrolled by both birds until the chicks were fledged from pair D's fourth nest. This dispute was the most serious of the few observed between neighbours. Boundary disputes were rare, because of the lack of neighbouring pairs.

Another type of trespassing occurred in which the trespassing birds were not challenged by the owner. This happened when adult birds were moving about with dependent fledglings. For example, male D moved throughout the lower part of territory G with his five fledglings (Figure 4.7c). Although male G sometimes sang near the loudly begging chicks he never approached them. The vigour with which an area is defended may depend on the phase of the breeding cycle the resident birds are at.

Territory size

The areas of territories between the two breeding seasons showed similar variability. Table 4.6 lists the areas of territories during the 1978 breeding season. Extensions to male D's territory are also included.

Table 4.6. Territory area during the 1978 breeding season.

Territory	Area (ha)	Territory	Area (ha)
A	0.49	F	1.40*+
B	1.03	G	0.96
C	1.22	H	1.39
D1	2.22*	K	0.72*+
D2	2.42	P	0.78+
D3	2.57	S	0.74+
D4	2.57	R	0.76*+
E	0.58*		

* same as prebreeding season area.
+ minimum area, as not all boundaries known.

4.7.2 Independent juveniles and immatures

This section covers the breeding and post-breeding seasons. Figure 4.8 shows the location of territories and birds during this period.

Movements after independence.

There was a marked contrast between the two breeding seasons as to the number of successful first nests. No chicks were fledged from the first nests of pairs A, C, D, G and H (and males B and E were bachelors). The only known successful first broods were in territories F and S, the other territories not being monitored over this period. These chicks became independent towards the end of November.

Because of the poor success rate for first nests no young birds were present in territories A to E, G and H, thus allowing the movement of juveniles away from parental territories to be monitored over a greater area than for the 1977 season.

No juveniles were sighted until 30-12-78 when a male was seen in territory D. A further male was sighted in the same territory on 5-1-79 and another in territory G on 8-1-79. By 12-1-79 call notes were heard along stream A. Again, as for the 1977 breeding season, there appeared to be a synchronous movement of some juveniles away from their parental territories about five to six weeks after independence.

Territories and movements.

After mid-January, juvenile tits were seen and heard moving throughout adult territories. Some birds maintained subterritories on the fringes of these territories as in 1977, whereas others moved about continually. Birds on subterritories emitted regular, loud call notes in response to other tits calling, and when trespassing occurred. No detailed observations were made on the duration of these subterritories as the delay between visits to the study area from

Figure 4.8

Territories are enclosed by the dashed lines.

Ⓐ streams.

unb. = unbanded.

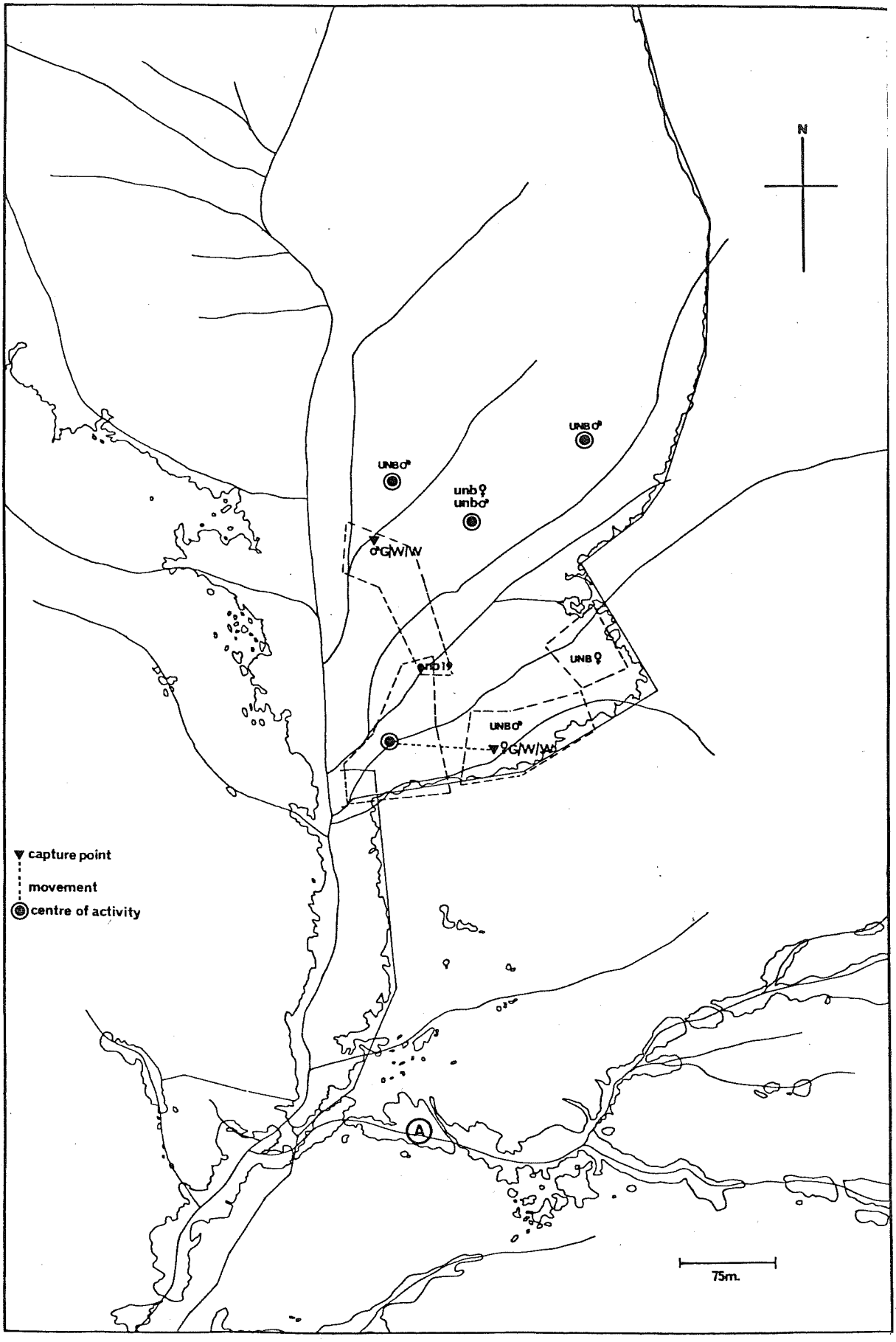


FIGURE 4.8 Juvenile - immature territories, January to April 1979

February onwards was too great to be sure the same unbanded birds were being seen in the same area each time.

However, some information was obtained from the five birds banded after the 1978 breeding season. Male G/W/W maintained a territory encompassing the shared boundary of territories D and G for a minimum of 10 weeks, after being banded on 8-2-79. Female G/W/W, banded in territory H on 11-2-79, shifted to another area and maintained a territory covering the southern part of territory D, for at least four weeks. This female was very vocal.

Territory H was divided between a juvenile male and female once the adults began moulting. At least two further juveniles were also present in the area. These birds may have been from the last brood of pair H.

Some areas contained concentrations of juvenile and immature tits, of which only a proportion were resident. For example, on 9-3-79, the following tits were observed in the area round nest box 19 (Figure 4.8): female G/W/W at the upper limit of her territory; male G/W/W and another unbanded male, these two birds chased each other several times; another unbanded male, which was moulting heavily, in the company of an unbanded female; an unaccompanied unbanded female. Of the six tits seen, only the two banded birds appeared to hold territory in this area.

During April the numbers of tits present began to decrease and subterritories also began to disappear. Adult birds which had completed their moult reasserted themselves in their territories, driving out resident immatures. For example, pair H were resighted in their usual territory in mid-April, having apparently driven out the immature male which had been resident at this time.

In contrast to the 1977 post-breeding season, few birds were resident along the main stream below territory D. This may have resulted from the poor breeding results for some pairs and hence the

smaller number of juveniles produced. One male, however, was found to be resident in an area not formerly occupied by tits. This was in the bush along the main stream adjacent to the shearing shed (Figure 2.4). He was first seen on 12-4-79 and moved about in this area over a 10 day period. He had no neighbours and was probably an immature male which had recently moved away from the study area. An unbanded male was also resident along stream A and was seen feeding out in the fields.

By the end of May, tit numbers appeared to have stabilized, with most birds on territories, but not reacting to a tape of a male song played within their territories.

4.8 1978 ADULT POST-BREEDING SEASON

Breeding activities ended at different times for differnt pairs, as for the 1977 season, with the adult birds becoming retiring as they began to moult. Female 111, resident in territory G, was recaptured on 8-2-79 but showed no sign of moult. She was not resighted after her capture. Pair H were resighted on 12-4-79 in their usual territory. No other adult birds were seen during the post-breeding season.

4.9 1979 PREBREEDING SEASON

Birds and territories observed over this period are shown on Figure 4.9.

Only two visits were made to the study area over this period. However, a territory shift of a banded female was recorded. On 8-7-79 female 133, formerly resident in territory H, was seen moving about with an unidentified unbanded male (possibly male H) along stream A. An unbanded male was also seen in territory H. By the 22-8-79, female 133 and the male were moving throughout the area covering former territories A, B and C. They also moved out into the fields searching

Figure 4.9

Territories are enclosed by dashed lines.

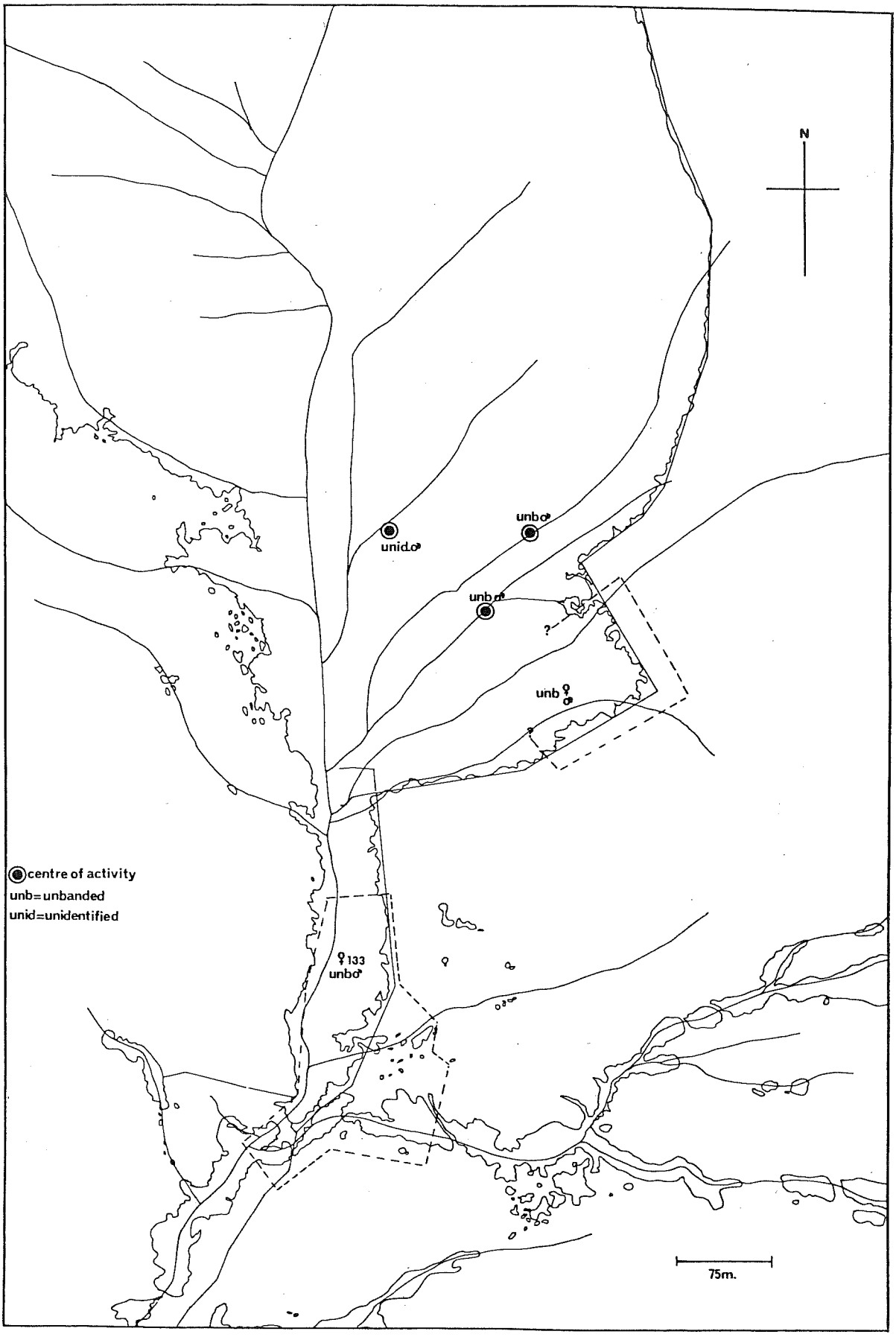


FIGURE 4.9 Territory location, 1979 prebreeding season, August

for food. Territory H was occupied by an unbanded pair of tits who were also feeding out in the fields.

Only a few sightings of tits were made in the main body of the study area, with little or no reaction to tapes of male song. The unbanded male resident adjacent to the shearing shed along the main stream in April was still present in late August in the same area. He was singing loudly and was recognized from his song.

4.10 SUMMARY AND DISCUSSION

The Yellow-breasted tit maintained a territory throughout the year, with territorial advertisement and defence peaking during the late prebreeding season and the breeding season. On completion of breeding, adult territorial activities ceased and were not resumed until April when the moult had been completed. During the intervening period, juvenile and immature tits moved throughout these territories unchallenged. Some of the adult territories were subdivided amongst several tits and were defended by their owners against other birds. Other tits moved about continually and did not defend a territory. As the post-breeding season progressed, the number of tits in the study area dropped so that by about late May the population had appeared to stabilize with nearly all birds on territories. The remaining birds appeared to be floaters.

Territorial advertisement and defence was low over the winter, probably being due to a balance between the physiological state of the bird and the climate. With an increase in the release of sexual hormones towards the breeding season, territorial activities began increasing to a peak again (Marshall, 1961).

The territorial nature of, and intolerance towards other tits was seen developing before the fledglings became independent (see

4.13 and Chapter 6). After independence, juveniles rarely associated with each other except if a pair bond was formed at this early stage. A proportion of juveniles settled on to subterritories after about two weeks and maintained them in the usual manner. Five to six weeks after independence there was a synchronous movement by some birds away from the adult territories. These birds occupied vacant or unclaimed areas and, along with those birds which took over an adult territory, appeared to have a greater chance of maintaining these territories and surviving to the next breeding season than those birds which set up small sub-territories on the peripheries of adult territories. Floaters had to wait until they could replace another bird on a territory or set up a territory of their own.

The low survival rate of banded birds from one season to the next is possibly indicative of the habitat in which they live, and also gives an indication of the number of birds fledged during the breeding season. Some possible factors affecting the distribution and density of tits in the study area are discussed in Chapter 10.

Dispersal of birds away from the study area continued into May. Not all birds appeared to be driven away. Although the study area is connected to a further patch of bush by the main stream, no tits were observed in this area during the two years followed. These birds were probably immatures; their fate was not determined.

Territory size varied between 0.49 and 2.57 hectares, but males did not patrol all parts of their territory regularly. Juvenile birds of both sexes maintained territories ranging in size from no more than about 0.10 ha up to the same size as the largest adult territories.

The minimum territory size necessary to give a pair the opportunity to breed successfully was about one hectare. A larger territory, however, did not guarantee success as nest abandonments and nest site selection also played an important role (see Chapter 5).

Territory size can be affected by several factors, including the vegetation type and density. In my study area, the largest territory had only scattered undergrowth whereas the smaller territories tended to have thicker vegetation. Therefore, territory size may be related to the distance the male's song travels through the vegetation.

Bisset (1978) calculated the area of a Pied tit's territory in the Hunua Ranges as 1.5 ha, using a grid system. Other estimates of territory size for the Pied tit have also been made. In rimu-dominated country in the Waitakere Ranges, territories ranged in area between 1.2 and 2.5 ha (Skinner, 1978). On Kapiti Island, Wilkinson and Wilkinson (1952) gave a figure of about 10 acres (4 ha) per pair. Potts (1884) estimated that there may be "six pairs nesting within an area of some twenty acres of suitable country" for the Yellow-breasted tit. On the Snares Islands, the Black tit had a territory averaging 0.22 ha (Flack, in prep., a).

In comparison to the tits, South Island robins in Kowhai Bush, Kaikoura, maintained a territory varying in size between 0.5 and 5 ha (Flack, in press), with an average of 2 ha (Flack, 1973). On islands, however, territories were much smaller. The territories of South Island robins on Outer Chetwode Island varied between 0.16 and 1.0 ha, with a mean of 0.42 ha. The Black robin had a mean territory size of 0.78 ha (range 0.32 - 2.03 ha) (Flack, in prep., a).

SECTION B

INTRASPECIFIC BEHAVIOUR

4.11 INTRODUCTION

The reaction of one tit to another varied, depending on the sex and maturity of the birds involved and the circumstances under which they met. Interactions were observed between birds of the same and opposite sexes and of all stages of maturity, from dependent fledglings to breeding adults. Aggressive incidents involving males were more commonly observed than those involving females.

This section lists and discusses the types of interactions observed during the present study. The displays and postures used during such interactions are also described. Dependent fledglings chasing after adults for food are not considered in this section (see Chapter 6).

4.12 THE CHASE AND FIGHT

The commonest interaction observed between tits of both sexes and all ages was the chase, which sometimes culminated in a fight. Not all chases were of an aggressive nature however, particularly when they occurred between the male and female of a pair (section 4.13).

4.12.1 Interactions between adults and independent juveniles

Adult male/juvenile male.

The commonest chases observed were between adult males and independent juvenile males during the latter part of the breeding season. They took place when an adult male saw or heard a juvenile while moving about his territory. Usually he would let out a few loud call notes, chase the juvenile for a new metres and then fly off.

An adult male reacted more aggressively if the juvenile was seen or heard near a nest site or dependent fledged chicks. After the loud call notes, which probably acted as a challenge, he chased the juvenile for at least 10 m. In some cases he would make repeated feinting dives at the juvenile which usually resulted in the juvenile flying off for a few metres. The adult male often sang a few phrases of song after such an encounter.

More rarely the male would persist with his attack on the juvenile. This sometimes resulted in a fight. The following example was the most extreme interaction observed: Initially, loud call notes were heard and then male 118 was seen pursuing a juvenile which kept fluttering out of his way. After three or four such encounters, male 118 flew at the juvenile and, after a brief chase lasting a few seconds, both birds fell to the ground with their claws entangled. After fluttering weakly on the ground for 15 seconds, they disengaged and flew up to some branches about one metre above the ground. The juvenile male then chased after male 118, hovering near him several times during the chase. Male 118 then chased the juvenile several more times but was unable to drive him off. Male 118 then started feeding nearby, and after the juvenile male flew off, he remained in the area and sang several phrases of song. Throughout the encounter, which lasted 10 minutes, the crest and body feathers of both birds were puffed up. The frontal spot of male 118 remained inconspicuous.

Juvenile males chasing adult males were rarely observed.

Adult male/juvenile female

Adult males seldom chased juvenile females, and usually ignored them. In contrast to the juvenile males, females always left the area after being chased by an adult male. No fights were observed. In one incident a female ended up on the ground after a chase but the male did not make contact with her. Juvenile females were not observed chasing

adult males.

Adult female/juvenile male.

Only one case was recorded. This occurred when a female chased off a male which had approached her too closely. The female's mate continued the chase.

Adult female/juvenile female.

Few encounters were observed and only brief chases of a few metres resulted.

4.12.2 Interactions between dependent siblings

Interactions between siblings were first observed a few days before they became independent. Males were involved in initiating nearly all the interactions seen. Chases and fights were common.

Male/male.

Interactions occurred when two males were moving about together searching for food. Then, for no apparent reason, one would chase the other. For example, after one male chased his brother they were seen struggling together for a few seconds on a branch. After separating, they continued searching for food, but 10 seconds later they were fighting again, resulting in their claws becoming entangled, with one male hanging upside down below a branch attached to the other perching on top of the branch. After breaking apart they resumed feeding.

During such interactions, either a staccato chuck was uttered or the birds remained silent.

Male/female.

Interactions between brother and sister ranged from chases to fights. The male always initiated such interactions, and several examples were recorded where both birds tumbled about on the ground with their claws entangled. Bill clicks, a sign of extreme aggression,

were occasionally heard.

In one case, a male kept trying to mount his sister as if trying to copulate. When she moved, he chased after her and both ended upon the ground, fighting.

Female/female.

A few chases of two to three metres were observed. Sisters were much more tolerant of each other than brothers.

Instances of mistaken identity were also observed, in which one fledgling begged off another. This occurred when one fledgling landed near another, resulting in the first bird begging off the new arrival. Females begging from males were more commonly observed than males begging from females. The typical begging posture and calls were given, but soon ceased when no reaction was gained.

4.12.3 Interactions between dependent fledglings and independent juveniles

In the cases observed, fledgling females begged for food off independent juvenile males. This resulted when a male moved too near the fledglings. A female would fly over to the male and immediately start begging. Usually the male chased her off or the female stopped begging after a few seconds. The appearance of a male appeared to be a sufficient stimulus to evoke the begging posture and calls.

4.12.4 Interactions between independent juveniles

These were some of the commonest interactions observed during the latter half of the breeding and post-breeding seasons, and demonstrated the development of intolerance towards other tits.

Male/male.

The commonest interactions were chases. Loud call notes were usually given before a chase took place. Chases between two males could

continue for up to about five minutes at a time, but no fights resulted from these chases, however. Calls given during the chases included call notes and staccato chucks. More rarely the birds were silent.

Male/female.

Chases were again the commonest interaction observed between males and females, with the number of observations in which males chased females, and females chased males, being similar.

For juveniles defending subterritories on the perimeters of adult territories, chasing was the usual form of defence. No fights were observed. Very loud call notes were sometimes emitted before a chase. Juveniles not resident on territories also chased each other regularly on meeting.

Female/female.

Interactions usually occurred between territory-holding females and intruding females. Birds sometimes came within centimetres of each other before a chase took place. Invariably the owner of the territory chased the intruder.

Chases between non-territorial females seldom occurred.

4.12.5 Interactions between adult birds and near-independent fledglings

When fledglings were approaching independence, adult birds could sometimes be seen selectively chasing particular numbers of a brood, while continuing to feed the other chicks. These birds were chased away as soon as they approached the fledglings still being fed. Adult males chased off male and female chicks, while females chased female chicks only.

4.12.6 General observations

The chases and fights described between juveniles were seen during the latter part of the breeding season and the first half of the

post-breeding season. Interactions between adults and juveniles were common only during the latter part of the breeding season. Chases between immatures, and immature males and juveniles, were also seen during the post-breeding season, but no fights resulted.

The population density was highest over the breeding and post-breeding seasons, and hence the greatest number of interactions took place during this period. As the post-breeding season progressed the number of birds present dropped, but even when birds did meet interactions became fewer and were less aggressive. In some cases the birds remained near each other showing no sign of intolerance. For example, during May 1978, three females foraged within a few metres of each other, eventually moving apart without showing any signs of aggression. The time of the year appeared to play an important part in the reaction of one tit to another.

4.13 PAIR CHASES

Pair chases were seen most commonly during August and early September for adult birds, and during February and March for some juvenile birds which had paired-off and were on territories of their own.

Pair chases involved the male chasing the female, but no contact was ever made between the birds. Chases were seldom vigorous and covered only a few metres. Normally birds would be feeding together before the chase and continued doing so after it had taken place.

Calls given during the chase by the male included call notes and staccato chucks (which are usually given in an aggressive context). At other times he remained silent.

During the breeding season several chases between a pair occurred in a more aggressive context near the nest site. The male chased the female and then attacked her so that they ended up struggling on the ground. One example involved two fights over a 30 second period. Initially the pair was seen locked together on the ground, the male holding on to the female with his claws. Bill clicks were also heard. After struggling together for five seconds they disengaged and flew about 10 metres where they were again seen locked together on the ground. On breaking away, the female flew back to the nest. The fights may have resulted from a misidentification of the female by the male, resulting in him treating her as an intruder.

The only occasion on which a female chased a male occurred during the breeding season when a pair was feeding nestlings. As the male flew off the nest after feeding the chicks, the female chased him for about one metre as she flew up to feed them. She may have mistaken him for an intruder.

The function of the non-aggressive pair chasing was not established but may have been part of the courting display (see also 4.15.1). The South Island robin also has pair chases, but these are much more vigorous than those seen in the Yellow-breasted tit. They can last for up to 4.5 minutes with the male always chasing the female (Powlesland, 1979).

4.14 ADULT MALES AND TERRITORY MAINTENANCE

During the late prebreeding season and breeding season, adult males maintained their territories in two ways. Firstly, and most commonly, they advertised their presence by singing loudly throughout their territory, and when they approached a shared border the neighbouring male often countersang if he was in the area. Some males sang from exposed perches in the canopy, as they moved about.

Secondly, they maintained their territories through chases, displays and fighting. These were only used when trespassing occurred or when boundaries were under dispute. The number of shared borders a male had (i.e. neighbours), and the aggressiveness of his neighbours, probably determined the frequency of interactions with other males.

When a bird trespassed into his neighbour's territory he usually remained silent and moved about in the more densely vegetated areas, i.e. he skulked about. If he was seen or heard by the owner of the territory, a challenge resulted. Loud call notes were exchanged (see Chapter 9) and the intruding male either flew off, was chased off, or stood his ground. If he refused to back down then a dispute resulted. The two birds approached each other to be about 30 cm apart, at any level of the vegetation profile except the ground. The two antagonists then stared at each other with their body feathers fluffed and crest feathers erect. After 15-30 seconds the intruder usually backed down and flew off. Otherwise the intruding bird was chased, with the owner giving staccato chucks. Often this was the only indication that a dispute had occurred. After an encounter, both birds sang a few phrases of song once they had moved apart.

Disputes which went beyond this stage were rare and occurred when two males disputed a territory boundary. Only one full-scale boundary dispute was observed. This took place when male D trespassed into male G's territory on 28-10-78 and would not back down on being confronted by male G. (Male D had been singing loudly in the area beforehand.) The males were about 20 cm apart, on a branch one metre above the ground, facing each other. Male G (the defender) held his wings out horizontally with the flight feathers spread so that the wing-bar was very evident. He maintained this pose almost constantly during the dispute. He also raised his wings slowly to about 40^{o} above the horizontal and then lowered them back slowly several times. His body feathers were fluffed

and his crest raised. Male D's crest was raised but his body feathers were not as fluffed as male G's. His wings were not held out horizontally. Throughout the encounter, constant loud countercalling was heard.

Most of the time the birds stared at each other while stationary. However, they also moved about from branch to branch. At one point they flew at each other and contacted with their claws. A staccato chuck was given before they broke apart. Short chases of up to five metres also occurred. Finally male D moved back into his territory and sang a phrase of song. Male G continued calling and sang shortly afterwards. During the dispute they had moved along what was later found to be their shared boundary (Figure 4.7c). The dispute lasted about five minutes.

A similar interaction has been described for the Pied tit. In this example, both birds fanned their wings and tail feathers (Bisset, 1978). Fighting between male Yellow-breasted tits has also been observed by Potts (1883), Buller (1888) and Philpott (1919).

4.15 FEATHER DISPLAYS AND STANCES

As shown in section 4.14, the erection of the body and crest feathers, along with wing fanning, played an important part in territorial defence and maintenance. A number of other displays and stances were also observed, both in aggressive and non-aggressive situations. Fleming (1950) summarized the displays of the five sub-species of tits. Aggressive behaviour included the raising and displaying of the frontal feathers, wing fluttering, and darting flights with arched wings, accompanied by bill snapping. Displays included wing quivering by the female, and chasing "butterfly flights" by the male, with wings spread awkwardly, high and forward. These displays were not described, however.

4.15.1 Body-feather displays

Displays involving the fluffing of the body feathers were seen in three different contexts. The way the body was held (the stance) and the calls given, determined the response of the other bird.

1) Aggressive Behaviour: these displays have been described in previous sections, but all involved a very upright stance while looking directly at the opposing bird.

2) A second type of display was observed only once. Its function was not understood. This occurred between the male and female of a pair on 16-7-78. Both birds were feeding together a few metres apart in the bush edge. The male flew out into the field and the female flew on to the fence along the bush edge. He promptly chased her back into the bush. She reappeared and was chased again. Then both birds reappeared on the fence about 30 cm apart. They had their crest and body feathers raised and countercalled continually. Both looked at each other and then turned their heads away, and then looked at each other again. After 60 seconds they flew back into the bush. The male sang 3 or 4 long phrases afterwards.

   This display was similar to that given by adult males disputing or defending territory.

3) Begging: when dependent fledglings or adult females begged for food they fluffed up their body feathers and also ruffled their wings. They crouched down on the perch with their head thrust forward and gave loud begging calls. When the male was doing the feeding, his crest was sometimes raised. Near-independent fledglings which did not give this posture on meeting the male were often chased. Therefore, this appeared to be a submissive posture.

4.15.2 Wing Displays

When a tit is perching on a branch its wings are held tucked against its body, drooping just below the tail. The wing-bar on the flight feathers is seen as an L-shaped bar (as in the frontispiece). Several displays were observed in which the wings were held in the horizontal or vertical planes, which resulted in the wing-bar being exposed to varying degrees. The body feathers were not fluffed. Wing-fanning in aggressive situations is described in 4.14.

Horizontal displays.

Solitary birds and members of a pair sometimes held their wings out in the horizontal plane for a few seconds, either holding them still or quivering them. These displays could be repeated several times in a row (up to nine times in one example). Occasionally the wings were held just above or just below the horizontal. Call notes, feeding chatter and song (in males) were given during the display which appeared to be a reaction to novel stimuli, such as the presence of myself.

Wing-flicking was performed by the male of a pair as the pair moved about within a few metres of each other, foraging. For example, a male flew to the trunk of a matai and flicked his wings in and out very slowly, three times, resulting in the wing-bar being exposed on the spread flights each time. This display was only seen when the male landed on a vertical trunk so that the dorsal surface of his wings were presented to the female who was usually only a few metres away. This may have been part of the courtship display. Similar behaviour has been observed in the Pied tit in which the male and female faced each other and flicked both wings alternately towards each other (Orenstein, 1979).

Vertical displays.

Displays involving the movement of the wings in the vertical or near-vertical plane were seen in individual birds, pairs, birds of both sexes, adult and juvenile plumaged birds, but not between birds of the

same sex.

During the late breeding season through to early winter, tits were seen drooping their wings in the vertical plane below their usual position. The flights were splayed revealing the wing-bar. The wings were either held still, or quivered. In some cases they were held out slightly from the body. Each wing-droop lasted 2 or 3 seconds. No vocalizations were given during these displays. They were sometimes given in conjunction with foot-trembling but the two may not have been related (see also section 8.2.4). Again, wing-drooping may have been a reaction to mildly alarming stimuli.

Two observations were made of a male which raised both his wings upwards to the near-vertical, and then quivered them. In both cases he was feeding dependent fledglings nearby, and on one occasion the chicks flew after him after the display. No function could be assigned to the display. It did not appear to be a stretching movement, sometimes seen after a bird had been sitting still for a while.

A partial distraction display was seen on two occasions, both occuring when I approached newly fledged chicks too closely. The male approached me and then flew off and stopped a few metres away. He raised one wing up in the vertical plane and quivered it, and then raised the other and quivered it. He repeated this 3 or 4 times. He remained quiet.

The full distraction display involves the wings being raised, fanned and quivered, with the tail also being fanned. Jerky, puppet-like actions on the ground also accompany the wing display (Buller, 1888; Soper, 1976). Similar displays have been described for the Pied tit (Parkin and Parkin, 1951; Wilkinson and Wilkinson, 1952). The positioning of the wings in the distraction display of the Australian Red-capped robin has been described by Immelmann (1960).

Figure 4.10

A male displaying an "alert" posture.

4.15.3 Postures

In its day-to-day movements, a tit characteristically perched at an angle of about 45^{o}, and had sleeked plumage with the frontal spot being a slit of colour above the beak.

However, when a bird was stimulated by a disturbing influence its posture and behaviour changed. If it was mildly aroused its crest was raised and the frontal spot sometimes flashed. Its stance became more upright and the bird stared in the direction of the disturbing influence. If it was further aroused, the breast feathers were fluffed. In more aggressive situations, further displays were used (see earlier sections).

The "alert" position was similar to the mildly aggressive posture, but the stance was almost up and down, with the neck stretched upwards. The breast feathers were fluffed and the crest raised (Figure 4.10). This posture was used when a male was observing a disturbance from a vantage point, usually 5 to 10 metres above the ground.

When investigating a tape recording of the song of another male, tits of both sexes flew rapidly about the source, rarely staying on one perch for more than a few seconds. The crest was usually raised, with the bird giving an aggressive posture. Juvenile males gave loud call notes. Similar behaviour has been noted in the Pied tit (Bisset, 1978). Birds also postured aggressively towards a cork rubbed on glass. This reaction was also gained by Poole (1951).

4.16 SUMMARY AND DISCUSSION

The Yellow-breasted tit used a number of behavioural mechanisms to maintain its territory and hence its isolation. Males sang throughout their territories and along their shared boundaries, to advertise their presence. When trespassing occurred or disputes arose,

displays were used to try and bluff the opponent into giving ground. Chases and fights occurred when these other mechanisms failed.

The intolerance of one tit towards another was most evident during the late breeding season and the post-breeding season when chases and, more rarely, fights took place between adult males and juveniles. Juvenile intolerance of other juveniles was also noticeable. Characteristic vocalizations were associated with these interactions (see Chapter 9).

Juvenile males and females maintaining territories were equally as vigorous in their advertisement and defence of that territory, but once the females had passed through the juvenile moult they became quieter and less aggressive than the males. They took no part in boundary maintenance activities during the breeding season. Immature males displayed territorial behaviour similar to that seen in adult males.

Displays, postures and vocalizations played an important role in determining the reaction of one tit to another. Begging calls and postures from dependent fledglings and adult females resulted in the male feeding them. Juveniles which did not beg were chased off.

Wing-drooping and spreading appeared to be associated with mildly alarming stimuli. Wing-fanning when given with an aggressive posture was seen during intense territorial disputes between adult males, whereas wing-flicking was used during courtship. The way the wing-bar was exposed during these displays was probably also important. Wing-drooping in the Silvereye is also associated with aggressiveness (Kikkawa, 1961).

The white eye ring in juvenile and adult females (see Chapter 7) may play an important role in aiding the male to recognize the female. The male has a black eye ring which is not visible against his black head plumage, although juvenile males sometimes have a few white feathers

in their black eye ring. It may have a signalling effect similar to that of the eyeline display in the Chatham Island Grey Warbler (*Gerygone albofrontata*) (Flack, 1975) and the Willie Wagtail (*Rhipidura leucophrys*) (Ives, 1975).

The frontal spot of both adult birds could be waxed and waned very quickly, thus serving as a signalling mechanism. It was often used in conjunction with the crest feathers, which in many species of birds are raised in response to nearly all mildly alarming or novel stimuli (Andrew, 1961). The function of the frontal spot and crest feathers has been investigated for the South Island robin (Flack, 1976b). During intraspecific interactions, the crown feathers were raised by dominant birds and the spot was often displayed by subordinate birds. In the present study the crown display was seen in tits in juvenile and adult plumage, on meeting another tit, and when adults were feeding nestlings and dependent fledglings. Too few observations were made to determine the function of the spot display in the Yellow-breasted tit. It was displayed, however, when a bird first appeared near a novel stimulus. Occasional examples were also recorded of females displaying their spot while begging off their mates, and in one instance the spot of a male was very prominent as he stared down into a nest of newly hatched chicks. Spot displays have also been described for the Pied tit (M'Lean, 1911). Bisset (1978) observed that the spot was displayed by both protagonists during boundary disputes.

The function of the frontal spot for the Australian Red-capped robin has been demonstrated (Immelmann, 1960). A cylinder of grey plasticene with a red cap evoked an immediate attack from a male robin. When a dummy with no red cap was used, no further antagonism was observed. This robin was also in immature plumage and lacked the red frontal patch, but could still recognize the red cap as a threat.

The Snares Black tit has no frontal spot. Intraspecific threat

involves chasing, wing-fanning and shaking, and the erection of the crown feathers of the head (Warham, 1967; Best, 1975), i.e. the same displays as seen in the Yellow-breasted tit.

Dependent fledglings reacted to the calls or presence of an adult tit by begging, but how they recognized an adult bird when it landed near them is not known. The colour patterns of the adult birds and their frontal spots may aid in recognition. However, dependent females sometimes reacted to the presence of independent juvenile males, which have an insignificant spot, by begging off them.

SECTION C

INTERSPECIFIC BEHAVIOUR

4.17 INTERACTIONS WITH OTHER SPECIES

The Yellow-breasted tit did not exhibit interspecific territoriality, i.e. it did not exclude other species from its territory. All encounters observed with other bird species took place during the summer, over the breeding season.

Tits chased individuals of only two species - silvereyes and grey warblers. Birds near nest sites and dependent fledglings elicited a stronger response from the adult tits than when they were encountered in other parts of their territory. The only form of interaction seen was chasing. Both sexes pursued intruding birds, with the male being involved in more encounters than the female.

The female reacted to the presence of other birds when they came too close to the nest. For example, a female was building a nest and was gathering nesting material a few metres away. When a grey warbler landed on the nest, the female let out several emphasized calls and chased the warbler off the nest for about two metres. She then

continued gathering nesting material. The call given by the female was heard only on this one occasion.

As in the female, the male seldom chased other birds. In one example, a male was feeding newly-fledged chicks when a silvereye landed about 30 cm from them. It was immediately chased off by the male. His frontal spot was not noticeably erect during this encounter. A juvenile male also chased a grey warbler for about three metres when it came too close to him. Male and female Pied tits also chased grey warblers (Bisset, 1978).

The majority of interspecific interactions took place when a tit was chased by another bird. Species observed chasing tits were blackbirds, bellbirds and hedgesparrows. Bellbirds were the most aggressive of these species and chased tits for distances of up to about 30 m. Only males were observed being chased by other species, and when being chased they let out loud, emphasized call notes which only stopped once the pursuit had ended. Male tits reacted strongly to the presence of bellbirds on occasions, and often let out loud call notes when a bellbird came within a few metres of the nest site. When bellbirds began singing near a male tit, he reacted by becoming silent.

Tits also reacted to the presence of other species by moving out of the immediate area. For example, a female was returning to her nest when a magpie (*Gymnorhyna tibiens*) landed in a tree a few metres away. She immediately flew off. On another occasion, the same female settled on to the nest but flew off 30 seconds later when magpies began calling nearby. Also, movement away was sometimes seen when a bellbird landed within a few metres of a tit. Normally when incubating, the female remained hunched down in the nest with only the eyes and tail being seen above the rim of the nest. She stayed this way even when another bird came within a metre of the nest.

A reaction was also observed towards the presence of the

Australasian Harrier (*Circus approximans*), an aerial predator. Both sexes reacted by emitting a loud alarm call which often continued after the bird had disappeared. On one occasion a male, feeding on the bush edge, gave approximately 80 consecutive alarm calls in response to a harrier. Similar calls were given when magpies were seen. The native pigeon also elicited a response. They were present in the study area only during March, April and May, and tits reacted to their presence as they did to a magpie. One juvenile male flew about rapidly, calling loudly, when a pigeon crashed through some flimsy foliage in the canopy. M'Lean (1911) recorded a male Pied tit attacking a morepork for 20 minutes. The reaction of tits to low-flying predators has also been noted by Hay (1975).

4.18 DISCUSSION

Interspecific encounters were only rarely observed. Usually when a tit was near a bird of another species, they ignored each other. Tits also tolerated other species nesting near them. In one case, a fantail nest was located 2 m from a tit nest, with both species feeding nestlings at the same time.

Bellbirds displayed the most aggressive reaction towards tits of all the species present. The aggressive nature of bellbirds towards other species has also been observed for the South Island robin. Flack (1976b) and Powlesland (1979) have observed bellbirds chasing robins, and also robins chasing bellbirds. These authors also noted vigorous chasing of tits by robins where these two species occurred together. Chatham Island tits have been seen chasing and attacking Black robins. The robins also chased the tits (Flack, in prep., a). When a tit attacked a robin, it displayed horizontal wings lifted to and above the horizontal, and also raised crown feathers.

The function of the spot and crown feathers during interspecific

interactions remained undetermined from this study. Other species may have chased tits because they came too close to their nest site. Bellbirds may be more aggressive because they may exhibit interspecific territoriality.

SECTION D

4.19 CONCLUDING DISCUSSION

In this section, some of the behavioural patterns of the Yellow-breasted tit observed in the previous three sections are summarized and discussed in relation to behavioural principles and patterns based on other bird species in the general literature.

Brown and Orians (1970) listed three characteristics which are essential before an area can be recognized as a territory:

1) It is a fixed area, which may change slightly over a period of time.
2) There must be acts of territorial defence by the possessor which evoke escape and avoidance in rivals. Such acts can be divided into:
   a) identifying acts that designate the defender and that make his presence conspicuous to his rivals, such as certain vocalizations and displays; and
   b) actual defence, such as attacking, chasing and threatening rival intruders.
3) Such acts result in the area becoming an exclusive area with respect to rivals.

Each of these characteristics was observed in the behaviour of the Yellow-breasted tit.

Pairs of tits, and bachelor males, centred their activities in the same area throughout the year. During the winter this area was sometimes expanded to include the surrounding fields if the birds were resident along the bush edge. Over the breeding season the area inhabited remained relatively constant, with pairs centering their activities about the nest site. Pair D was the only pair which showed any major range extensions during the breeding season; the extensions being related to the placement of successive nests. Where birds did shift to a completely new part of the study area, they once again moved about a fixed area.

Both categories of territorial defence were used to defend the area against intruders and rivals. Self-advertisement, using song and calls, was the first line of defence. When this failed to maintain the exclusiveness of an area, displays and vocalizations associated with threat were used. The final line of defence involved chases and, more rarely, fights. After aggressive encounters both males usually sang a few phrases of song. Adult females took no part in boundary defence, although they sometimes moved along the boundaries with their mate. Therefore, the behaviour of the males resulted in an area being used exclusively by one male or a pair of tits.

The territory a tit occupied corresponded to Hinde's (1956) type A territory, i.e. "a large breeding area within which nesting, courtship and mating, and most of food-seeking takes place."

In birds in the Northern Hemisphere which are resident on a territory all year round (i.e. non-migratory), periods of high territorial intensity (spring and autumn) alternate with periods of low intensity (summer and winter) (Klomp, 1972). This pattern of intensity probably results from an interaction between the physiological state of the bird with its external environment (Marshall, 1961). In the Yellow-breasted tit, the intensity of territorial behaviour was not

as rigidly defined as this. Territorial maintenance activities were at a peak during the late prebreeding season and for much of the breeding season, with least activity during the post-breeding season while the birds moulted, and during winter. A slight resurgence in singing occurred during April.

During winter, song was rarely heard and no boundary disputes were observed. When neighbouring birds did meet, they usually ignored each other. Therefore, some sort of innate spacing mechanism must have been present to enable birds to maintain their isolation. The simple call notes given by tits as they moved about searching for food may have assisted birds in knowing where their neighbours were, and hence avoiding them.

Five to six weeks after independence, some juveniles undertook a synchronous movement away from their parental territories. This apparently innate dispersal mechanism has also been observed in juvenile birds of other species at various periods after fledging. Great tits (*Parus major*) and Blue tits (*P. caeruleus*) dispersed almost explosively from the area in which they were fledged about six weeks after independence (Lack, 1954) while Black-capped chickadees (*P. atricapillus*) dispersed rapidly after the family unit dissolved about three weeks after fledging occurred (Weise and Meyer, 1979).

The distance a tit dispersed could only be established by tracing the movements of birds banded as nestlings. As only one bird was banded as a nestling and disappeared while still being fed by the adult birds, dispersal distance of independent juveniles could be calculated only from their movements away from their point of capture. Birds which were resident on territories the next breeding season travelled straight-line distances varying between 75 m (male 126) and 375 m (female 207) (Figure 4.4). This can be compared with a median distance of dispersal from birth to first breeding site of 558 m and 879 m for male and female

Great tits, respectively, in Wytham Wood (Greenwood *et al.*, 1979). The median dispersal distance for Black-capped chickadees was 1.1 km (Weise and Meyer, 1979).

After the first movement away from adult territories, juvenile and immature tits continued to appear in areas where they had not been seen previously, up until about May. Several theories have been put forward to explain this dispersal. These are detailed in Greenwood *et al.* (1979). Population density and interactions with other birds have been invoked to explain the continuing dispersal of juveniles and immatures from an area. This may be the case for tits which set up subterritories on the periphery of adult territories. They may be driven out by males reclaiming territory after moulting. Dispersing individuals have often been assumed to be inferior members of the population, suffering a higher mortality than those which do not disperse. This appears to be the complete opposite to the situation in my study area. Those birds which shifted to vacant areas probably had a greater chance of surviving to the next breeding season than those birds which were later displaced from their territories on the peripheries of larger territories. Therefore, movement away from adult territories may be initially due to an innate mechanism and later on, population pressures.

A small proportion of juveniles did not set up territories during the late breeding season or the post-breeding season. These floaters may have moved about until they found a vacancy in a territory. At the start of the 1977 breeding season, possibly two males and one female were floaters. The males were not seen again after their capture, but the female was later found in a territory in another part of the study area. No floaters were known to be present at the start of the 1978 breeding season. If floaters were present at the start of the breeding season they did not appear to survive it, as territories which were

abandoned during the course of the season were not reoccupied.

Usually the presence of floaters indicates a high population density, in which there are not enough available territories for the birds present, i.e. birds are prevented from breeding due to dominance and the competition for space (Brown, 1969; Brown and Orians, 1970). This is the situation on Outer Chetwode Island for the South Island robin where some birds fail to occupy a territory or develop breeding behaviour in their first year (Flack, in prep., b).

The high number of floaters present in some populations has been demonstrated by removing resident birds and observing the recolonization rate (e.g. Stewart and Aldrich, 1951). In most cases nearly all the surplus birds are males. The problems of interpreting the role of a floater in a population are discussed by Brown (1969) and Rappole *et al.* (1977).

CHAPTER 5

NEST SITES AND NESTS

5.1 INTRODUCTION

This chapter examines the range of sites used, the types of nests built, and the variety of nesting materials used by the Yellow-breasted tit. The use of nest boxes is also discussed. Building procedure and the behaviour of birds while building are covered in Chapter 6.

Not all nests of all pairs could be found, even when it was known that a particular pair was breeding. This was due, in the main, to the difficulties experienced in following some pairs through parts of their territories because of the steep and broken terrain and the almost impenetrable shrub layer. For other pairs, even when the approximate location of the nest was known, the nest often could not be found because of the secretiveness of the birds or, again, the impenetrability of the vegetation.

To find nests, the birds were followed until they flew back to the nest. During nest-building, the female was the easiest to follow as she was moving to and from the nest all the time, but when she was incubating the male was followed as he brought food into the nest area to feed to her.

5.2 NEST SITES

During the two breeding seasons 16 nests were found, the sites of which could be categorized according to the type of vegetation supporting them. Table 5.1 summarizes the information in this section.

Table 5.1. Summary of nest sites and nests located.

Pair	Location	Site type	Nest type	Height (m)	Aspect	Success
1977						
1 nest 1	Tree fern	4	B	1.75	NE	✓
2 nest 1	Lawyer	3a	A	4.0	E	✓
2 nest 2	*Griselinia*	2a	-	6.0	E	x
2 nest 3	*Fuchsia*	1	B	3.0	S	✓
3 nest 3	Dead trunk	2a	A	3.0	W	x
5 nest 3	*Griselinia*	1	-	7.0(approx.)	*	✓
unknown	*Griselinia*	1	B	3.0	S	x
1978						
A nest 1	Lawyer	3a	-	3.0	not exposed	x
D nest 1	Tree fern	4	B	2.0	E	x
D nest 2	Hall's totara	1	-	8.0	*	x
D nest 3	Lawyer	3a	-	5.0	N	x
D nest 4	*Griselinia*	1	A	5.0	SW	✓
G nest 2	*Griselinia*	1	-	5.0	*	x
H nest 1	Pepper tree	3b	B	3.0	SE	x
H nest 2	*Fuchsia*	2a	B	4.0	SW	x
unknown	Tree fern	4	B	1.75	S	x

* not known, ✓ successful, x unsuccessful
- nest not recovered.

Four categories of nest site were recognized:

1) Hole or cavity in a well-established tree

Six nests were found in holes or cavities formed by rotting, subsequent to the loss of branches from the tree trunk or from a main branch. Two examples are illustrated in Figures 5.1 and 5.2.

Some tree species were more prone than others to this mode of cavity formation and very few species in the study area provided such sites. The main species involved was the Broadleaf, because in its mature and post-mature form it was often very gnarled, with a combination of rotten, dead and hollow limbs providing many possible nest sites. Such sites were often high in the tree and difficult to locate. Fuchsias, which predominated throughout the study area, also provided a few nest cavities. However, because most of the fuchsia was

recent second-growth, it was often very spindly, having only a few side-branches which were capable of leaving a cavity large enough to allow a nest to be built. A third group of species which offered possible nest sites were the podocarps. When over-mature and dying, these trees provided potential nest sites because of limb loss. Again, because podocarps were poorly distributed within the study area and many were less than 100 years old, few sites were available. All these species could, however, offer sites when not fully grown, through premature limb-loss during storms or a heavy snowfall.

No nests were located in holes in other tree species. Although *Pennantia corymbosa*, narrow-leaved lacebark, pepper trees and *Pittosporum* spp. formed part of the canopy, they rarely provided cavities because their branching system did not contain large side-limbs such as those found in broadleafs, fuchsias and podocarps. Other species which had a parasol-type canopy when mature, e.g. five-finger, were too open to provide sheltered nest sites.

Nests built in holes or cavities were open only to the front with the sides, back and roof forming a protective shell. Despite being well-protected, the amount of camouflage afforded by the sites used varied from nest to nest.

Four of the nests were built in broadleafs, and one each in a fuchsia and a Hall's totara. Broods were successfully fledged from three of these nests, with three nests being recovered.

2. Ledge or fork in a tree

Two subcategories were recognized on the basis of the positioning of the nest in the tree.

a) Ledge on a branch or trunk.

Two ledge-nests were found. They were built in the rotted-out ends of trunks or branches. Ledge sites were less sheltered than cavity

sites because protection was gained only from the sides. One ledge-nest had two side entrances (Figure 5.3).

One nest was built in the top of a rotten vertical trunk and the other in the rotted-out end of a dead fuchsia branch. Neither nest was successful.

b) In the fork of a tree.

One nest was found in a fork formed between the main trunk of a broadleaf and the stub of a broken-off side-branch. Partial protection was provided by a side-branch above the nest, with the only protection from the side coming from a hanging fern *Asplenium flaccidum*. This nest was not successful.

Both subdivisions were characterized by poor overhead protection and a varying amount of protection from the side.

3. Located in vines or shrubs

Some nests were built in vines or in shrubs. Vegetation of this type did not provide a solid base for nests. These nest sites were markedly different from the previous two types of sites.

Further subdivision of this category of nest site could be made on the basis of the type of vegetation involved.

a) Built in a bush lawyer tangle.

Three nests were built in bush lawyer tangles and were supported by a base of interwoven stems, which were suspended from, or supported by, the branch of a tree. These nests were built just under the canopy, where the bush lawyer leaves formed a continuous cover over and around the nest. They were extremely well camouflaged and hence difficult to detect (Figure 5.4).

A brood of chicks was successfully fledged from one of these nests.

Figure 5.1

Cavity in a broadleaf (nest removed).

Figure 5.2

Cavity in a fuchsia. Note the built-up front of the nest.

Figure 5.3

Ledge site (nest removed).

Figure 5.4

Typical nest site in a tangle of bush lawyer.

Nest location indicated by solid triangle.

Figure 5.5a

Nest on the side of a tree fern.

Note the long tail of basal material.

Figure 5.5b

Close-up of the same nest.

b) Built in a shrub

Only one nest was found in a shrub. It was built near the top of a bushy, four metre high, pepper tree on the bush edge. The base of the nest was supported by several small branches, with the sides encasing the two main trunks of the pepper tree. The nest was extremely well camouflaged and was found only by following the female back to the nest site over a two week period.

This nest was not successful.

Both types of nest were very well camouflaged, but although they appeared to be well-protected they were, in fact, more vulnerable to changing weather conditions than sites in the other three categories.

4) Built on the side of a tree fern

This site was very different from the previous three categories and demonstrated the ingenuity of the tit in being able to utilize any potential nest site. This type of nest site has not been described previously.

Three nests were found attached to the trunks of tree ferns. They were built on one or two upturned, dead, broken-off frond stems; there being no other point of attachment (Figure 5.5a,b).

All the nests were protected from above by the downhanging dead fronds of the tree fern, which also gave some side protection.

Only one of these nests was successful.

Although four broad categories of nest sites were found in the study area, the published literature demonstrates that an even wider variety of sites can be used by the tits. These include: under the heads of cabbage or ti trees (*Cordyline australis*) (Buller, 1882; Potts, 1884), in the walls and roofs of buildings (Potts, 1883; Anglesey, 1957), amongst strips of peeling bark (Guthrie-Smith, 1914),

and in the roots of an uprooted tree (Potts, 1882). Potts (1884) has even recorded a nest built in an old teapot. The Nest Record cards for the Yellow-breasted tit show a similar variability in nest site choice, and include additional sites such as under the lip of an overhanging earth bank, under rock faces, and in a cliff face. Table 5.2 shows the sites used according to the Nest Record cards. Only the first five categories were found in my study area.

Table 5.2. Nest site choice based on results from the Nest Record cards.

Site	Number	%
Holes in trees	16	38.0
Ledges in trees	8	19.0
Forks in trees	3	7.1
Bush lawyer	2	4.8
Tree vegetation	1	2.4
Holes in rock or ground	7	16.7
Roots of upturned tree	2	4.8
Building	2	4.8
Peeling bark	1	2.4
Total	42	100

The Pied tit demonstrates a similar variability in nest site selection but fewer data are available (Reischek, 1887; M'Lean, 1911; Wilkinson and Wilkinson, 1952; St. Paul, 1976; Nest Record cards).

The Yellow-breasted tit, therefore, is capable of building a nest in a wide variety of sites. The features these sites have in common are that they are usually well-camouflaged and often well-protected.

The commonest sites used in my study area were those located in holes or cavities, or ledges in trees. Despite the small number of nests located (16), 50% (8) came under this classification. This is

a trend also seen from the results of the Nest Record cards, where 24 of 42 sites located (57%) were in similar sites. If the category of holes in rocks or the ground, which did not occur in my study area, is added, a total of 73.7% (31) of the nests were built in holes or cavities of some description. This suggests that tits may choose a cavity-type of nest site in preference to other types if one can be found at the time of nest-building. However, if such a site is not available they can successfully utilize a number of other types of sites. The preference of tits for building in holes has also been noted by Buller (1882), Andersen (1926) and Soper (1976).

5.3 NEST HEIGHT

Nests found in the study area ranged in height from 1.75 m to 8.0 m above the ground (Table 5.1). The highest nests were built in emergent trees (broadleafs and podocarps) but were not built above the level of the lower continuous canopy. Nests built in bush lawyer were located just under the canopy where leaf cover was thickest. The lowest nests were situated on tree fern trunks.

Figure 5.6a shows the distribution of heights for nests found during this study. The mean height was 4.06 m, with a distinct grouping of nests below 6 m. This can be compared with a mean height of 5.08 m for nests recorded on the Nest Record cards, in beech forest (*Nothofagus* spp.) (Figure 5.6b), with a grouping of nests below 7 m. If records from other sites in other forest-types are included, increasing the sample size to 42, the mean is 5.31 m. Nest heights varied between ground level and 18.2 m. This is probably a good guide to the range of heights over which the Yellow-breasted tit will build in mature beech forest, which can reach a height of 30-35 m (Poole and Adams, 1964). In my study area the height range available for potential sites was compressed, as the canopy height averaged about 8 m.

FIGURE 5.6a HEIGHT OF NESTS ABOVE GROUND IN THIS STUDY.

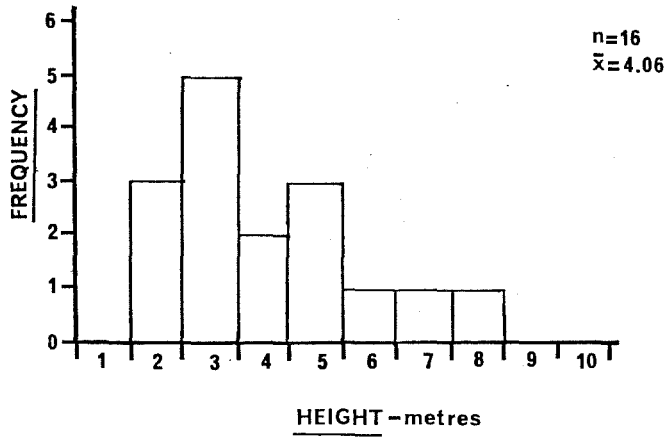
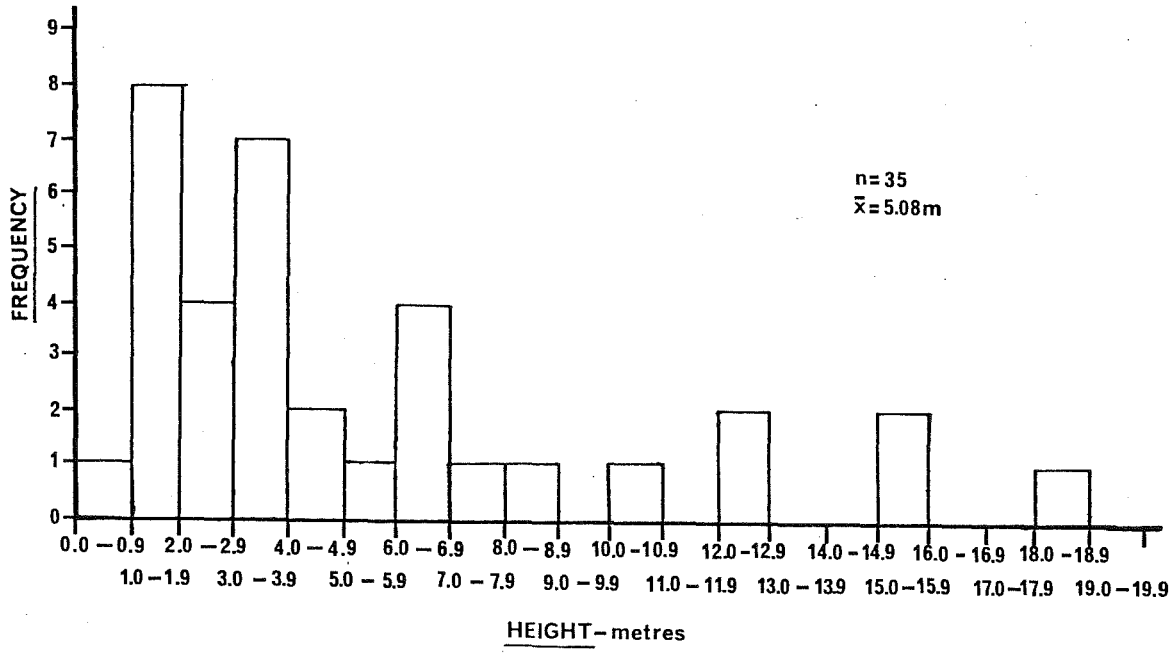


FIGURE 5.6b HEIGHT OF NESTS ABOVE GROUND IN BEECH FOREST (from O.S.N.Z. Nest Record cards)



Comparison of the two histograms shows that they have a similar shape, with distinctive clumping in the lower heights and a tail up to the greater heights where fewer nests are built. This suggests that nest sites are selected for, which fall in the lower strata of the vegetation profile.

This preferred range is similar to that for heights in the published literature. Guthrie-Smith (1914) gives a range of 7-14 feet (2.1 - 4.2 m) and Soper (1976) gives a range of all heights up to 12 m. The Pied tit shows similar preferences: 8-10 feet (2.4 - 3.0 m) (Reischek, 1887); and 9-12 m in a wet season, but lower in a dry season (St. Paul, 1976). The Nest Record cards give a range of 0.6 - 4.8 m.

However, nests at lower heights are easier to locate than higher, inaccessible ones, so there may be a bias towards the lower nests.

5.4 NEST ASPECT

The prevailing wind during the breeding season at Mount Fitzgerald (September to February) was from the north-east, with occasional changes to the north-west and south-west (Laing, 1918; pers. obs.). Wind intensity ranged from very strong winds, which buffeted even the main side-limbs of the emergent trees, down to light breezes, which only just rustled the leaves. Strong winds from the south-west were usually accompanied by driving rain. On rare occasions calm conditions prevailed, usually for no more than a few hours at a time.

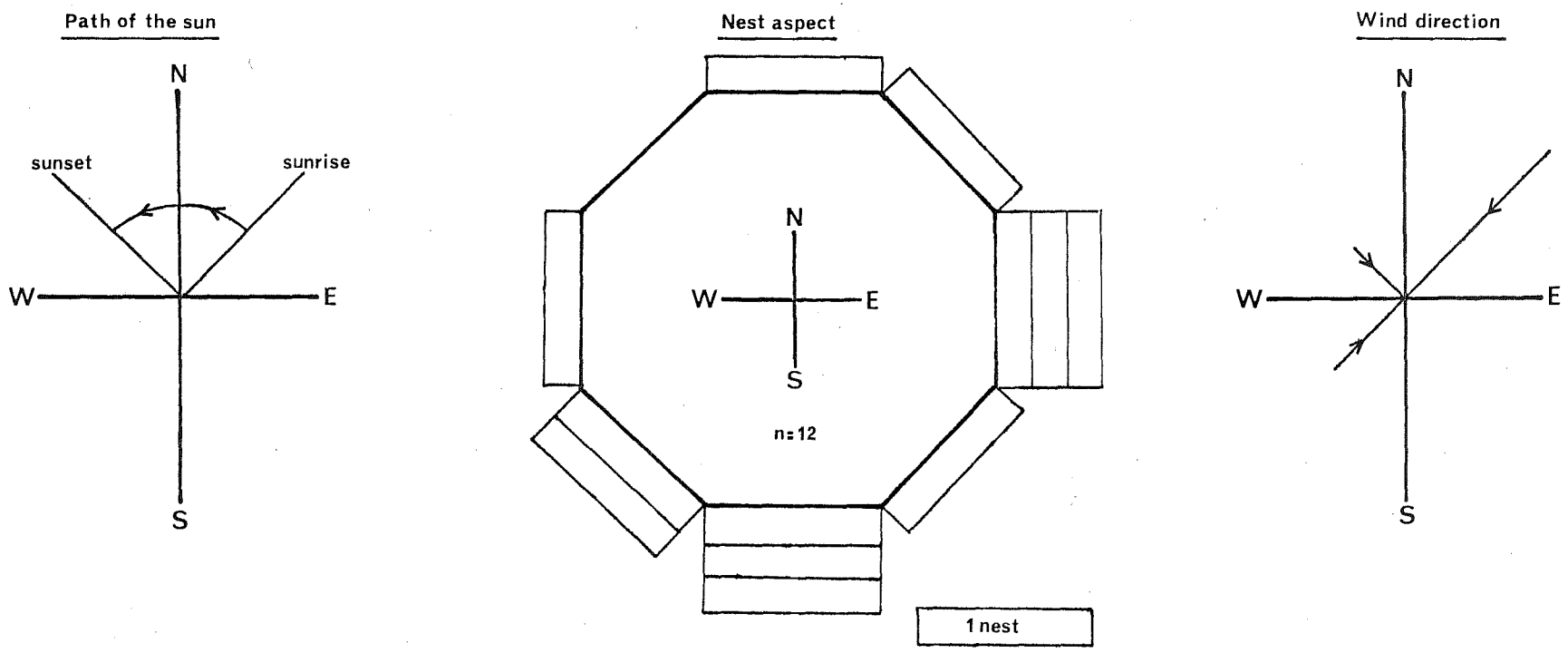
If wind and weather conditions are an important factor in determining nest aspect, then tits might be expected to select sites facing away from the prevailing winds, so that the nest and its contents would be afforded more protection. Nests built in or near the canopy were probably more vulnerable to changing weather conditions than those situated below the canopy in more sheltered sites. Lower nests were

protected from all but the strongest winds and rain, whereas nests built in bush lawyer, in or near the canopy, were less secure and were buffeted by strong winds and rain (pers. obs.). Nests in cavities had more stable support and more protection, but could still be affected by the weather. For example, Reischek (1887) found a Pied tit's nest in a cavity, into which rainwater had drained. One nest in the present study was destroyed by strong winds. It was built in a shrub on the bush edge and was torn apart during a weekend of very strong winds, at first from the north-west and then from the south-west. Potts (1873) noted that the nests of the Yellow-breasted tit were often well-concealed, but were often blown out by gusty winds.

In this study, the direction in which 12 nests were facing was determined (Figure 5.7 and also Table 5.1). Although the sample size was small, nests appeared to be built facing away from the prevailing wind. If an arc is drawn from the north-east, counter-clockwise to the south-west, the predominating winds over the breeding season fall between these two limits. Only three nests fell within this arc. However, despite this, both nests facing into the south-west were successful. Gill (1979) found that of 91 Grey Warbler nests located in Kowhai Bush at Kaikoura, 61% faced either north-east, east, or south-east. The prevailing wind was from the west (Grey Warblers build a penduline nest).

A nest which was recovered three months after five chicks had fledged from it demonstrated the effect of the weather. The nest faced into the south-west and all that remained of it was a pile of soggy, compacted moss with slightly raised sides. In contrast, nests recovered from below the canopy in more sheltered sites showed few signs of deterioration.

FIGURE 5.7 NEST ASPECT, WIND DIRECTION & PATH OF THE SUN.



Nest placement appeared to be unrelated to the path of the sun. Because of the surrounding hills, the sun did not appear over the study area until it was in the north-east, and disappeared in the north-west. Only two nests were found in this arc.

Therefore, nest placement may have been influenced by the predominating winds, but because the general availability of potential nest sites and the direction in which they faced was not known the relationship remains unclear.

5.5 NEST STRUCTURE AND MATERIALS

Because the Yellow-breasted tit builds nests in such a variety of sites, the nest-type might be expected to vary between sites. This was true only to a limited extent. The nest was always cupular, with the main difference being in the amount of material used to build it. A typical nest is shown in Figure 5.8.

There are two main parts to a tit's nest - the basal platform which provides anchorage and support; and the cup which is placed in, or on, the platform and provides warmth, protection and camouflage. These are features common to the nests of many species (Welty, 1975).

Two broad categories of nest-type were recognized on the basis of the amount of basal material used during construction (see also Table 5.1).

A) Nests with little or no basal material

Nests in this category were characterized by having very little or no basal material. If any was present it did not have a supportive function. These nests were not confined to any particular type of site but were commonly found in hole or cavity-type nest sites.

B) Nests with varying amounts of basal material

The amount of basal material in these nests varied from a layer just thick enough to give some type of support, up to a substantial base which encased most of the cup. Nests with this type of base were built in sites which required a levelling of the floor of the cavity to enable the cup to be built more easily, on the sides of tree fern trunks and in tangles of bush lawyer where the supporting stems were insufficiently intertwined to form a solid base.

The quantity of basal material used depended on the physical nature of the site chosen. Cavities in trees often had a near horizontal floor, so that a large quantity of supporting material was not necessary to provide a steady base. In such cases, either the nest cup only was built, or a very thin layer of coarse basal material was laid down first. This layer had no supportive function and may have been instinctively placed in the nest site when building was initiated. Conversely, material may have already been present in the chosen site.

Where the floor was uneven, or did not meet the requirements of the female, the basal material was built up until a suitable base was formed. In one site, where the front of the cavity was too open, material was placed in the gap until a flat base was obtained (Figure 5.2).

When building in bush lawyer, the amount of basal material used was determined by the density of entanglement of the stems which supported the nest. Loose entanglements required more material.

Nests built on a tree fern trunk were the bulkiest nests found in the study area, as they contained the greatest amount of supportive material. Such a quantity was required to provide a stable base so that the cup could be safely supported. These nests had a long tail of material hanging below them, similar to that found in the nests of fantails.

Once a base of coarse material had been formed, the cup was built and was either placed on top of the base or built down into it. In both cases the base material and cup remained as two separate layers, i.e. there was little or no intermixing of the materials which made up the two layers.

The base and cup were built of different materials and constructed in different ways. The base was composed of coarse litter, heaped up until a suitable base resulted. There was no interweaving of the materials. Materials used in the base included dead leaves, small twigs, bark scraps (including strips of fuchsia bark), bush lawyer petioles, crumbling rotten wood, pieces of moss and lichen, dead fern leaf tips, ground fern roots and, more rarely, tree fern scales. These were sometimes mixed with cobwebs and other miscellaneous material from the litter layer.

In contrast, the cup was constructed of tightly compressed mosses intermixed with tree fern scales and the occasional dead fern leaf tip. In the ten nests recovered, the cups were composed of the same materials and constructed in the same way. This suggests that such materials were selected for, and also reflected the general availability of these materials in the study area. In two nests in the same territory, tree fern scales were not used, probably because there were no tree ferns in the immediate vicinity of the nest sites.

Table 5.3 lists the mosses commonly found in the cups.

Table 5.3. Mosses found in nest cups.

Species	Habit and Site
Weymouthia mollis	Veils hanging from branches.
Brachythecium rutabulum	Thick patches on branches.
Acroladium chlamydophyllum	Dense clumps on soil and logs.
Neckera pennanta	Loose hanging patches on bark.
Dicranoloma menziesii	Epiphytic on tree trunks, tufted.
Lembophyllum divulsum	Dense mats on bark, soil and roots.

Weymouthia mollis was the commonest moss found in the cups and was used almost exclusively in some nests. It was very common in the damper regions of the study area, growing in veils hanging from branches and trunks. Other mosses frequently used were *Acroladium* and *Neckera*, both of which dominated in some nests. The dominant mosses used were of the "small-leaved" varieties. Coarser mosses with larger leaves, such as *Bracythecium* were used only very occasionally. In addition to tree fern scales, ground fern scales (primarily *Polystichum* spp. and *Blechnum* spp.) were also used, but only rarely.

The outside of the cup was often decorated with coarser material, similar to that used in the base. This material was tucked into the moss and probably aided in camouflage. Decorating materials included liverworts (including *Lophocolea* sp.), pieces of bark (particularly fuchsia), mosses, and bush lawyer petioles. On some nests, lengths of lawyer petioles (up to 85 mm long) were incorporated into the rim of the nest. In areas near the bush edge, lengths of grass stems were used occasionally. The rims of some nests were coated with spiderwebs.

The inside of the cavity was lined with feathers. No other materials were used for this purpose. Two nests were found which lacked a feather lining, suggesting that either the female could not find any at the time of building, or did not use them in the nests she built. The number of feathers used probably depended on the number the female could find at the time. One abandoned nest contained 12 feathers from a variety of species.

Feathers from song thrushes, blackbirds, male and female tits, bellbirds and magpies were identified. Others remained unidentified. Feathers were occasionally seen scattered about on the ground, and in one example a group of 16 feathers from a female tit was found.

Lining the cup with feathers is a common practice in tits. Examples on the Nest Record cards include feathers from the kea

(*Nestor notabilis*), parakeets, and kiwis (*Apteryx* spp.). Feathers of the domestic fowl have also been used (Barker, 1883). Other materials which have been used as lining include ribbonwood bark (*Hoheria populnea*) (Buller, 1888) and the down of seeds (Reischek, 1887).

Little variability is exhibited in the choice of nesting materials. Moss is the common choice, usually with a mixture of other materials. One nest, from the Kaingaroa State Forest, built in a *Pinus radiata* tree, consisted of straw, pine needles and tree fern scales (Nest Record card 6455).

The size of the nest depended on the site chosen for construction. Those built in a limited space, such as in some cavities or on a small ledge, were limited by the available space. Table 5.4 lists the dimensions of selected nests.

Table 5.4. Dimensions of selected nests.

Nest site	Nest type	External Dimensions: front to back × breadth × depth (cm)	Internal Dimensions: front to back × breadth × depth (cm)	Cup depth (ext.)	Weight (g)
1	A	11.0 × 14.0 × 6.5	—	6.5	—
1	B	11.0 × 11.0 × 9.0	4.0 × 4.0 × 2.5	8.0	39.0
1	B	14.0 × 10.0 × 9.0	4.0 × 4.0 × 2.5	8.0	45.0
2a	A	15.0 × 9.0 × 6.0	5.0 × 5.0 × 3.0	6.0	35.5
2a	B	9.5 × 6.5 × 8.0	3.5 × 3.5 × 1.8	4.5	68.8 (base 51.3)
4	B	16.0 × 16.0 × 16.0	6.0 × 6.0 × 3.0	6.0	76.0
4	B	10.0 × 11.0 × 20.0	4.5 × 5.0 × 3.0	6.0	55.0

The nest with the smallest internal dimensions (2a, B) was abandoned shortly after the clutch of five eggs was completed. When the fifth egg was laid it sat on top of two others, leaning against the side of the cup, because the first four eggs filled the cup. The cramped conditions may have caused nest abandonment.

Apart from the above case, the internal cup measurements showed little variation, probably being directly related to the sitting position of the female. Similar measurements have been recorded by Potts (1884) 2.5" across × 1.5" deep (6.35 × 3.80 cm) and M'Lean (1911) 2.25" across × 1.0" deep (5.7 × 2.5 cm).

The dimensions which varied the most were wall thickness and the depth of the base. External cup depth showed little variation.

Dry weights of the nest varied considerably. The bulkiest nests, however, were not necessarily the heaviest. Nests with large quantities of rotten wood in the base were heavier than those containing more moss and fuchsia bark. If the average weight of a female is taken as 11.5 g (n = 17), then the nest weight to female body weight ratio varies between 3.0 and 6.61. This compares with an average value of 1.32 for the Grey Warbler (Gill, 1979).

5.6 NEST BOXES

In an attempt to facilitate observations on breeding activities, nest boxes were erected in different parts of the study area. Their design was based on one supplied by the Ecology Division of the D.S.I.R. These boxes had been used successfully by Pied tits in the Orongorongo Valley, Wellington. Sixty-one nest boxes were nailed to trees, two to three metres above the ground. They were erected during September 1977, and left for the remainder of that season and the 1978 breeding season.

Only a few of New Zealand's bush birds have been known to nest in

artificial nest sites. These include the Rifleman (Gray, 1979), Pied tits (Gibb, 1961; Nest Record cards), and the Snares Black tit (Best, 1975).

Unfortunately, none of the nest boxes erected during this study was used, and no nesting material was found in any of them. Three possibilities why the boxes were not used are:

1) the design was unsuitable,

2) the sites chosen were not suitable, and

3) natural nest sites were not limiting.

The first two possibilities can be discounted, as the Pied tit and Black tit have nested in boxes of similar design, placed in similar situations. The third possibility seems to be the most probable.

In Europe, nest boxes have been used extensively to increase numbers of hole-nesting, insectivorous birds, particularly tits (*Parus* spp.) and flycatchers (e.g. *Ficedula* (= *Muscicapa*) *hypoleuca*, the Pied flycatcher). They have been particularly effective in pine plantations where natural nest sites are scarce (Gibb, 1961). Von Haartman (1971) placed nest boxes in areas where Pied flycatchers were formerly absent and showed that nest sites, and not food, were limiting.

European results suggest, therefore, that when natural nest sites are limiting, artificial sites will be used. Gibb (1961) erected 100 nest boxes in Kaingaroa State Forest (which is dominated by *Pinus* spp. and *Pseudotsuga taxifolia*) and found that the only birds which used them were Pied tits. However, only a few boxes were used and these were often in groups, suggesting that one pair was responsible for building in several boxes. None of the boxes erected by Skinner (1978) for Pied tits, in the Waitakere Ranges, was used. Low rates of nest box utilization have also been shown by the Black tit (Best, 1975).

These results, in conjunction with the results from this study,

suggest that artificial nest sites will be used only when natural sites become limiting. Because the Yellow-breasted tit (and other tits in the genus) can use such a wide range of site types, this situation may never arise.

5.7 DISCUSSION

The ability of the Yellow-breasted tit to build nests in a wide variety of sites is a feature common to other members of the tit assemblage in New Zealand, e.g. the Pied tit and Snares Black tit. Sites used by tits on the Snares Islands included hollow logs, holes in trees, vegetation, and around the perimeter of the island tits were found nesting just over the edges of cliffs, on ledges (Stead, 1948; Best, 1975).

When selecting a nest site, a pair of Yellow-breasted tits did not choose any one type of site over another, for consecutive nests. For example, one pair which built four nests used a site on the trunk of a tree fern, a hole in a totara, a tangle of bush lawyer, and a cavity in a broadleaf.

The Robins, which are the other main line of *Petroica* stock in New Zealand, also build in a range of nest sites. South Island robins nest from 2.1 to 23 m above the ground, with most nests being on dead stumps, in forks, in cavities left by fallen limbs, or on ledges provided by thick curling vines (Soper, 1976). At Kowhai Bush, Kaikoura, however, the robins normally built in a fork between the main trunk and a branch of a tree, and not in enclosed cavities (R. Powlesland, pers. comm.). Therefore, site selection probably depends on the type of vegetation present and its structure.

Where robins and tits occur together, vigorous interspecific display has been observed (Flack, 1976b). This interspecific rivalry

may also occur in nest site selection in some areas. In general, however, tits nest higher up in the vegetation than robins (Soper, 1976), so such rivalry may be minimized by this separation. Robins will also build on the nests of other species, a phenomenon rarely observed in tits.

When the range of sites used by the Yellow-breasted tit is compared with that of the Australian members of the genus, some similarities can be seen (Table 5.5).

Table 5.5. Australian members of the Genus *Petroica* - nest sites and materials.

Species	Total length (mm)	Nest site and Height (m)	Materials and internal cup dimensions (mm)
Flame robin *P. phoenica*	135	Tree forks, hollows in trees, clefts in rocks and creek banks, roots of upturned trees and rafters of buildings. 0 to 19	Grass and bark strips bound with cobwebs. Lined with soft material. 47 × 38
Scarlet robin *P. multicolor*	130	Vertical forks, or horizontal boughs, or hollows. Usually below 5 m. 0.5 to 19	Bark strips, moss, grass, cobwebs, decorated with charred wood and lichen + soft lining 38 × 31
Red-capped robin *P. goodenovi*	115	Tree forks, usually near the ground. Shape varies according to site. 0.5 to 10	Fine grass, rootlets, moss, cobwebs, soft lining. 38 × 31
Rose Robin *P. rosea*	110	High in tree forks. May build in same fork in following years. 1 to 20	Fibres, moss, bound with cobwebs, soft lining. Decorated with lichens. 40 × 30
Pink Robin *P. rodinogaster*	130	In low vegetation. Usuallly under 5 m but up to about 7 m.	Fibres bound with cobwebs and draped with lichens. Also moss. 47 × 32

This table is constructed from information contained in the following references: Howe (1932), Chisholm (1960), Stewart (1965, 1977), Officer (1969), Macdonald (1973).

The Flame robin shows a greater adaptability than any other Australian robin in the choice of nest sites (Chisholm, 1960). It nests in a similar variety of sites to the Yellow-breasted tit, and also over a similar range of heights. The Flame robin also seems to prefer sites with overhead cover (Officer, 1969).

CHAPTER 6

THE BREEDING SEASON

> "Reproduction is the part of the life cycle with the greatest environmental dependence .... Every species is apparently adjusted to breed at the time of the year at which it can raise its young most effectively."
>
> - Immelmann, 1971

6.1 INTRODUCTION

During the two breeding seasons monitored, the behavioural biology of adult and juvenile tits was followed for all phases of the breeding cycle. Fewer data were gathered on laying and hatching dates, and the physical development of nestlings, because all the nests located during this part of the cycle were inaccessible.

Where direct observation of the nest contents was not possible two methods were employed to determine the approximate timing of, for example, laying and hatching. Firstly, if any date in the laying to fledging phase of the cycle was known, then dates for the other parts of the cycle could be calculated by using figures given in the literature (see separate sections for references). For example, if the fledging date was known, then to find the laying dates the average lengths of the nestling and incubation periods were subtracted from this date. Secondly, it was possible to detect when egg-laying and hatching occurred by noting the changing behaviour patterns of the adult birds during each part of the cycle. By combining the results obtained from these two methods an accurate estimate of the timing and duration of the incubation, nestling and dependent fledgling periods was gained.

This chapter covers, in separate sections, the period from when activities associated with breeding begin, through to the independence of the fledglings. A general discussion comparing the results with those for other members of the genus concludes the chapter.

6.1.1 Preliminaries

The approach of the breeding season was marked with increased singing and territorial activities by the males during August. Courtship feeding was also observed. When the members of a pair moved about their territory together searching for food, at irregular intervals the male flew over to the female and fed her. When he approached the female with a food item she responded giving the typical begging response - crouched posture and head forward, beak open and fluttering wings. This was usually accompanied by begging calls. The begging calls of the female were heard more often than the event was seen.

During the nest building and incubation phases, the male fed the female more regularly and at more regular intervals (see later). She may have obtained a significant proportion of her food from the male over this period.

The earliest date on which feeding of the female by the male was observed was 20-8-78, a date similar to that recorded by Potts (1870). Philpott (1919) observed feeding as early as the first week in August.

Nest site selection was not seen during this study. However, it has been observed in the Pied tit (Wilkinson and Wilkinson, 1952) and the South Island robin (R. Powlesland, pers. comm.). In both cases the male attracted the female's attention to a possible site by calling to her, whereupon she often flew over and investigated it. Several sites could be examined before one was selected. It is not known if the male assisted in site selection if the female renested while he was feeding the previous brood.

6.2 NEST BUILDING

6.2.1 Commencement and duration of building

The start of nest building was marked by the female restricting her activities to the general area of the nest site. Females in territories bordering on the bush edge disappeared completely from this area.

In 1977, nest building started about 8 September. No observations were made on the first nests of this season. The earliest date on which building activities were seen for the 1978 season was 7 September, when a female was seen several times, moving about with tufts of moss in her beak. Three other females were all building between 10 and 15 September. No first nests of the season were observed being built after this date. Other pairs were also known to have commenced building, but their nest sites could not be located.

These building dates infer synchronous breeding. First nests of the season for all pairs were built over about a 10 day period.

A starting date during early to mid-September appears to be common for the Yellow-breasted tit, with Potts (1870, 1884), Anglesey (1957) and Soper (1976) all recording starting dates over this period. The Pied tit may start breeding activities during late August in some parts of its range (Wilkinson and Wilkinson, 1952; Bisset, 1978). Potts (1870) observed nesting material being carried as early as 26 July and nest building in mid-August for the Yellow-breasted tit. Nests begun in August, however, appeared to take much longer to build than later nests and were usually abandoned during construction or after completion.

In this study, nest construction from start to finish was not observed but all nests probably took no longer than five days to build and possibly as few as three. There was no difference in construction time between first and subsequent nests. Potts (1883) and Anglesey

(1957) recorded a building time of three to four days. Building time would also be influenced by the quantity of basal material gathered by the female (see Chapter 5).

6.2.2 Nest building procedure

Nest building procedure has been poorly described in the literature, with only a few details on the gathering of materials being published. For example, Potts (1883) described the behaviour of the female when selecting materials, and the duration of visits to the nest while building. Stead (1948) and Nest Record card 11,571, gave the steps in construction, from the forming of the initial circle of grass in the nest site to the placing of the feather lining, for the Snares Black tit.

Observations were made on the building of 10 nests over the two seasons, with the majority being found at about the half-completed stage. In cases where the nest could not be found, the behaviour of the female while gathering nesting materials was recorded.

Only the female built the nest. She was not assisted at any stage by the male. The nest building procedure was similar for all the nests on which observations were made, the main differences between the nests being the quantity of basal material brought to the nest site before the cup was constructed (see Chapter 5). Therefore, some females devoted more time and effort to this stage than other females. The basal part of the nest was constructed first, being composed of a matrix of mainly coarse material, whereas the cup which was built after the base was completed, was composed of much finer materials.

Building materials were gathered from the litter layer up to about five metres above the ground. On one occasion a female was observed removing moss from the trunk of a totara 10 m above the ground. The majority of material was collected from the litter layer and the

one to two metres above it.

The richest source of basal material was the litter layer where the heavier, coarse debris collected. Other sites often investigated for such material were knotholes which acted as traps for materials, and around the bases of ferns.

Finer materials for the cup, such as mosses, were gathered from all types of substrates. Tree fern scales were collected from all parts of the trunk, but particularly in amongst the bases of the dead fronds. The female often disappeared up in between the hanging fronds, reappearing 10 to 30 seconds later with a beakful of scales.

While collecting material, the female moved about rapidly from site to site with materials being gathered in a circle of up to 20 m diameter about the nest. During the construction of the base of the nest, the female brought in wads of miscellaneous, tangled material which sometimes hung for three or four centimetres on either side of her beak. In some cases the material appeared to be so bulky that she was just able to fly off with it. Her movement sometimes resulted in pieces breaking off. After the material had been selected, she either flew directly to the nest or paused briefly on a perch before doing so. On entering the nest she either dropped the material and flew off, or remained to arrange it into place. Time was spent arranging materials only after several brief trips had been made to the nest.

When searching for finer materials such as mosses, the female carefully inspected all possible moss-bearing surfaces, including old logs, rocks and tree trunks. To remove the moss from the site selected she tugged at it until a large beakful was obtained. Potts (1883) described her action as she tugged at the moss - she secured a firm hold with her claws and, using her spread wings as a brace against the trunk, she tugged repeatedly, with an upwards and backwards movement of the head. Despite the effort put into removing moss, she appeared to be

very selective, often discarding it and flying to another site.

Some areas were visited more often for materials than others, as they contained more suitable materials. Repeated visits were sometimes made to the same site.

When building full-time, the female returned to the nest every 5-15 seconds with up to eight trips per minute. On remaining to arrange and place materials in the nest, particularly when shaping the cup, she could be heard and seen rustling about, fluffing her wings and body feathers to mould and press the materials into position. (Nest Record card 6821 records the same procedure for the Pied tit.) The female spent between 30 and 45 seconds on the nest arranging materials.

Although she did not build continuously throughout the day, she could build for several hours at a time. In one example, a female built continuously for 2.5 hours, the entire length of the observation period. Often after the female had made several trips to the nest she disappeared for 10-20 minutes and then reappeared and continued building.

When the cup was nearing completion the female sometimes flew back to the nest with individual pieces of moss. These may have been specially selected for the internal lining of the cup and were possibly more difficult to find than other nesting material. When the cup was completed the feather lining was added.

Feathers were collected either singly, or several at a time. When a patch of feathers was found on the ground the female returned to the same spot until she had removed all of them. In one example, a female returned at least three times to the same spot, flying off with three or four feathers each time. On one occasion, she hopped about on the ground to pick up several scattered feathers. The feathers were either pressed into place by the pressure of the female's body or tucked into the moss lining of the cup. Two nests were recovered which lacked a feather lining, possibly because the female could not

find any feathers at the time.

Some females placed cobwebs on the rim of the nest, and most nests had pieces of bark and lichen placed on their outwards-facing wall.

The only time females were regularly observed on the ground for more than a few seconds at a time was when they were gathering nesting materials. This occurred particularly when they searched around ground fern stems. Periods on the ground lasted no more than two minutes.

Some nests were difficult of access. For example, female D's first nest was on the side of a tree fern, and to get up to it she had to flutter vigorously up amongst the dead, down-hanging fronds obstructing her entrance.

When the nest was completed the female left it and did not return until egg-laying commenced.

6.2.3 Male activity during nest building

The male did not remain around the nest site while the female was building, but moved throughout his territory. On occasions, however, he approached the nest area and emitted call notes or a few phrases of song. The female answered with call notes, and when he remained in the area they often countercalled. The female intermittently let out quiet and medium call notes even when the male was not present. Usually when the male came near the nest site he was going to feed the female. In response to his calls the female stopped what she was doing, flew over to a perch and was fed. Sometimes she gave a begging posture and calls, but often the male fed her directly, with only a few begging calls being given.

After being fed, the female either resumed building or flew off with the male. If she flew off with him, she was fed several times by the male, returning to the nest site after 10-20 minutes. Feeding

intervals were irregular, varying between 10 and 60 minutes. When the female moved off with the male she also searched for food by herself. Whenever the female stopped nest building activities, she moved round with the male and not by herself.

Over this period, therefore, the male moved about his territory and fed the female at irregular intervals.

6.3 EGG STAGE

6.3.1 Delay before laying

After the completion of the first nest there was a delay until the first egg was laid. During this period the female moved about with the male throughout their territory and seldom came near the nest site. The female was fed at regular intervals by the male but also searched for food by herself. When both birds moved about together they emitted quiet countercalls and tick calls (see Chapter 9).

Over this period the female appeared to move about in a higher level of vegetation than usual. She was seen regularly in the 4-5 metre level and seldom approached the litter layer in the search for food. This behaviour pattern could not be quantified.

The delay before the appearance of the first egg after the completion of the first nest varied between 6 and 11 days. The length of the delay was not observed directly because the exact finishing dates of nests were not known. Therefore, delays were calculated from the earliest date on which nest building was not observed, up to when the first egg appeared. Similar delays before laying have been recorded on Nest Record cards 1101 (at least 8 days) and 10,367 (at least 6 days). For the Black tit a delay of 5 to 7 days has been recorded (Nest Record cards 11,571 and 72) for probable first nests.

For subsequent nests the delay was shorter, and varied between

one and four days. Potts (1883) and Anglesey (1957) recorded laying on the day the nest was completed. A delay of three days for a probable replacement clutch was noted by Stead (1948) for the Snares Black tit.

Eggs were laid at 24 hour intervals, and incubation usually started with the laying of the last egg, but the female of one pair was known to be incubating after the laying of the fourth egg of a five egg clutch. Incubation before the clutch was completed was also observed by Potts (1873).

6.3.2 Clutch size

Clutch size varied between three and five eggs, with four being the average. During this study a nest was recovered from which a brood of five was fledged. Pushed into the base of the cup was an egg. This implies that a six egg clutch can be laid. Nest Record card 9307 for the Pied tit records five eggs and one chick in a nest. Despite this, a six egg clutch or brood of six chicks has never been reported in the literature and may occur very infrequently.

Clutch size cannot be estimated from the number of chicks fledged because not all the eggs of a clutch hatch. Eggs can also disappear from a nest during incubation. Table 6.1 records the clutch sizes from cards of the Nest Record scheme.

Table 6.1. Frequency of clutch sizes from the Nest Record cards.

No. of eggs	Yellow-breasted tit	Pied tit
1	0	0
2	0	0
3	3	4
4	11	8
5	4	2
6	0	1*

* five eggs, 1 chick.

Only records on which the female was observed incubating the eggs are included.

Four egg clutches are common (Potts, 1869, 1884; Soper, 1976). Anglesey (1957) recorded a five egg clutch.

6.3.3. Egg colour and dimensions

Eggs are white with yellowish-purple spotting concentrated at the larger end. Full descriptions of eggs can be found in Potts (1869), Buller (1882), Andersen (1926), Fleming (1950) and Oliver (1955). A nest containing five eggs is shown in Figure 5.8.

Table 6.2 gives the dimensions of some eggs collected during this study.

Table 6.2. Egg dimensions

Pair H, nest 2	Pair 3, nest 3	Pair D, nest 4
18.0 × 14.7	18.9 × 15.8	unhatched egg
17.9 × 14.9	19.6 × 15.6	18.0 × 14.5
17.5 × 14.6		
17.7 × 14.7		
17.9 × 14.6		

All measurements in millimetres.

6.4 INCUBATION

6.4.1. Duration of incubation

The incubation period was taken from when the female laid the last egg up to the hatching of the eggs, and has been documented as lasting between 15 days (Soper, 1976) and 17 days (Potts, 1883; Anglesey, 1957).

None of the nests located during this study was accessible enough to allow the exact incubation period to be determined. Three clutches were found for which the laying dates of the last egg were known, but these were later abandoned during incubation. However, as incubation normally commenced with the laying of the last egg, an abrupt change in the female's behaviour pattern took place at this time. She stopped moving about the territory with the male and restricted her activities to the nest site. By noting when this change occurred and the first occasion on which the male flew up to the nest with food to feed the nestlings, an average incubation period of 16 days was calculated.

6.4.2 Male and female behaviour during incubation

Incubation was carried out by the female only. The male was never observed on the nest, either when the female was incubating or when she was away from it. He usually only approached the nest area when he was going to feed her and seldom came within three to four metres of the nest when doing so. If he was not going to feed her he remained silent.

Female behaviour on the nest

While the female was incubating on the nest she remained hunched down into the cup so that only the top part of her head and her eyes were visible over the rim. Her tail sitting out the back of the nest was the only other part of her body that was visible. She did not react to the presence of other birds perching or feeding near the nest.

The female did not remain immobile while on the nest, but was seen moving about periodically. Such movements included standing up and then resettling facing in another direction, preening and ruffling the feathers, and on one occasion a female stood up, peered down into the nest and resettled and repeated this three more times. These were probably comfort movements.

Sometimes, when the male came near the nest area and let out call notes or song, the female raised her head and looked in the direction of the calls.

Feeding behaviour

During incubation, one of the main activities of the male was bringing in prey to feed to the female. For the rest of the time he moved about his territory, sometimes singing subsong while searching for food, and when near his shared borders, singing full song. However, all his activities were centred about the nest site.

When the male approached the nest area with the intention of feeding the female he signalled his presence to her. A variety of calls was given, but usually consisted of call notes or phrases of song. In response, the female did one of three things: she answered with a few call notes and flew off, gave some begging calls before leaving the nest, or waited for up to two minutes and then flew off. Usually she flew off the nest immediately on hearing the male calling, reacting to his presence when he was within 8-10 m of the nest. At other times, when the male was searching for food within a few metres of the nest, he exchanged calls with the female without her leaving the nest. The emphasis placed on the calls by the male may be an important factor in determining the action of the female. In addition, she may not have left the nest until she had sighted him as he always approached the nest from its most open side.

On leaving the nest in response to the male's call, the female flew to a perch usually within five metres of the nest. The male then flew over and fed her. More rarely she flew directly over to the male and was fed. She often flew to the same branch for six or seven consecutive feedings.

The typical begging posture was not given on every occasion. When the male fed her, a brief twitter was often heard as he placed the

food into her beak. This was usually drowned out by her begging calls.

After she had been fed, the female did one of three things:

1) She returned directly to the nest and continued incubating. If this was the case then the male flew off immediately after feeding her.
2) She flew off with the male and moved about with him in the general area of the nest site. In between the several times he fed her, she searched for food. No begging postures or calls were given when this course of action was taken. After a short period she left the male and flew back to the nest area, where she either flew on to the nest immediately or continued searching for food around the nest site, and then returned to the nest.
3) Most commonly she flew back to the nest site, after the male had flown off, and searched for food by herself. Her method of searching differed from the usual hunting technique, which involved scanning from a fixed point (see also Chapter 8), in that she moved quickly through the vegetation, remaining at one vantage point for only a few seconds. Quick darting flights to pick up a prey item were regularly made. After a few minutes she flew back up to the nest.

When approaching the nest, she did not fly on to it directly but flew cautiously from branch to branch until she reached the level of the nest. She then flew on quickly and settled down. On one occasion when a female was about to fly on to her nest she was frightened away by a magpie which landed in the vegetation about 3 metres away. Shortly afterwards, the same female flew off her nest after having been on it for 30 seconds when magpies began calling in a totara about 10 m away.

When flying up to the nest the female usually remained silent, but intermittently she was heard to sing a few phrases of quiet song. This was the commonest situation in which the female was heard singing.

Very rarely the female did not leave the nest when called off by the male. This occurred when the male flew off after feeding her and she remained off the nest searching for food. By the time she had returned to the nest and settled down, the male had come back with more food. She did not leave the nest if she had been on it for less than about 30 seconds.

Feeding behaviour differed when a pair had fledged a brood, and the female had renested and relaid. Because the male was busy feeding the chicks of the previous brood, he did not visit the female at regular intervals with food. This meant that she had to hunt for nearly all of her own food until the fledglings became independent, usually after about one week of incubation. Feeding behaviour then returned to normal. At irregular intervals, however, the male left the fledglings and flew to the new nest site and called the female off and fed her. They then flew off together for a few minutes, during which time the male fed the female. After splitting up, the male returned to the fledglings, and the female to her nest.

Nest attentiveness of female

As the female was fed by the male away from the nest, she did not incubate continuously. To determine if there was an incubation pattern present, continuous observations were made on incubating females, using a stop-watch to time their activities. Two representative examples of the results obtained are shown in Figure 6.1a and b.

The incubation pattern was determined by the feeding rate of the male. Whenever the male approached the nest area, it was usually with food to feed to the female. On two occasions in Figure 6.1a, however, the female left the nest without being called off by the male. This happened after two incubation periods of 40 and 49 minutes. Therefore, there appeared to be a maximum time period which the female stayed on the nest and after which she flew off whether the male was present or not.

Figure 6.1

Nest attentiveness of female D at 10 days and 8 days incubation.

•——• female incubating.

• for male indicates arrival at nest area to feed female.

Table 6.3. Nest attentiveness of female D.

FIGURE 6.1 NEST ATTENTIVENESS OF FEMALE D, 3rd NEST.

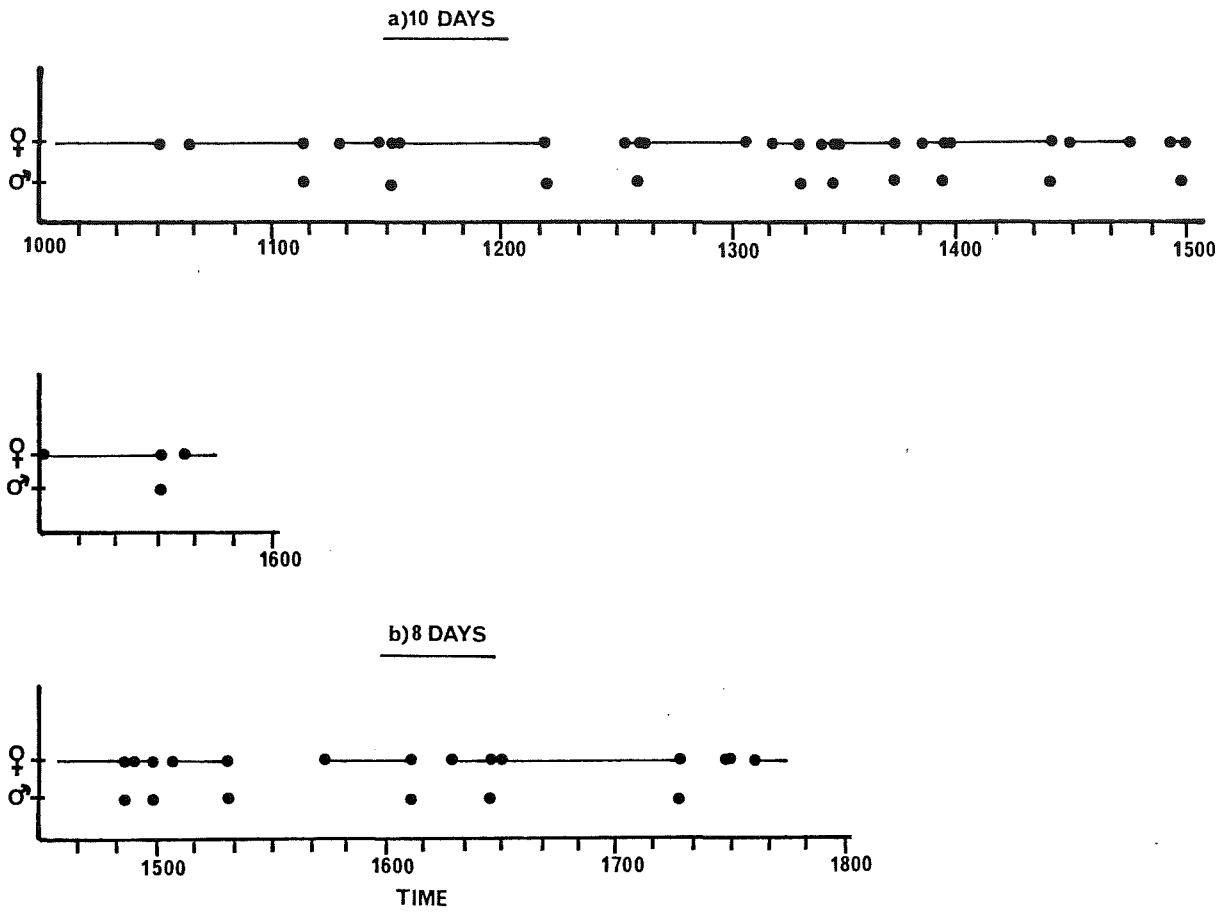


TABLE 6.3 NEST ATTENTIVENESS OF FEMALE D, 3rd NEST.

DAY	OBS. PERIOD (mins)	TIME ON NEST (mins)	% OF TIME ON NEST
10	335.0	241.5	72.0
8	180.0	133.0	73.0

	DAY	RANGE (mins)	MEAN
TIME ON NEST	10	0.5 - 40.0	15.1
	8	1.0 - 49.0	16.6
TIME OFF NEST	10	0.5 - 20.0	6.2
	8	1.0 - 16.0	6.7

On both occasions she searched for food by herself and then returned to the nest. The maximum period she stayed on until called off by the male was 30 minutes.

The minimum time female D spent on the nest was 30 seconds, and on one occasion she did not leave the nest when called off by the male because she had only returned to it about 20 seconds beforehand.

Time off the nest varied between 30 seconds, when the female returned to the nest immediately after being fed by the male, and 20 minutes. During this time the female was either fed by the male or searched for food by herself. Mean time off the nest is shown in Table 6.3.

Among species in which only one parent incubates, the bird usually allocates between 60% and 80% of its daytime activity to incubation. To achieve a higher rate the bird must be fed on the nest or be able to find food expeditiously during its recess from the nest (Welty, 1975). In the two examples given in Figure 6.1, the female spent an average of 72.5% of her time on the nest (Table 6.3). This can be compared with an average of 68% for the Grey Warbler (Gill, 1979) and 81% for the South Island robin (R. Powlesland, pers. comm.). The nest attentiveness rate in the South Island fantail averages between 90 and 98% as both sexes incubate (Ude Shankar, 1977). Factors which can influence nest attentiveness include ambient temperature and rainfall.

6.5 SUCCESSIVE AND REPLACEMENT CLUTCHES

6.5.1 Renesting after fledging

On the successful fledging of the first brood, both adults fed the fledglings. After one to three days the female left the feeding to the male and moved off to build the next nest. The gap between fledging and renesting varies, however, as Stead (1927) recorded a

female building the morning after fledging, whereas Wilkinson and Wilkinson (1952) recorded a 10 day delay before renesting took place in a pair of Pied tits.

The time to build the nest was the same for the first nest of the season, but there was a shorter delay between completion of the nest and the production of the first egg (see 6.3.1). On completion of the nest, and during laying, the female did not join the male and assist in the feeding of the fledglings. The male did visit her on occasions, however, during which he fed her several times. After the fledglings had become independent, the male fed the female more regularly.

6.5.2 Replacement clutches

If the first nest of the season was abandoned, then renesting took place. In six cases the females were observed building at a new site within one to two days of abandonment. Behaviour of the male and female remained the same as if the nest was the first of the season. Therefore, within 10 days of abandoning her previous nest a female could be incubating her next clutch.

There was no pattern in the siting of replacement nests. They could be built within 10 metres of the abandoned nest or in another part of the territory. This was also true for a nest built after a successful fledging.

Causes of nest abandonment were varied and in some cases could not be established. One nest built on the side of a tree fern was preyed upon by a mustelid. In addition to the broken egg shells, there were also 40-50 feathers scattered in the nest, suggesting that the female may have been initially trapped on the nest. This was the only example of predation seen. The female that lost this nest was observed rebuilding the next day.

The other main cause of nest desertion was probably the weather.

One nest was destroyed after a weekend of strong south-west winds and in at least two other cases the females were found rebuilding after several days of strong winds. Parkin and Parkin (1951) also found that a female Pied tit abandoned its nest after sitting through a weekend of violent storms and gales.

During the two breeding seasons, fifteen nests were known to have been abandoned. This included two nests, recovered from a previous season, which contained the remains of egg shells. Fourteen of these nests were abandoned during the incubation stage, and the other may have been preyed upon shortly before the chicks were due to fledge.

6.5.3 Number of successful broods in a season

Fourteen broods of dependent fledglings were located over the two breeding seasons, but because observations were not made on all the nests of all the pairs, the true nesting success could not be determined.

The number of nests built before a brood was successfully fledged varied. One pair was successful only on their fourth attempt and later abandoned their fifth nest near the end of the breeding season. Other pairs which had a successful first nest often abandoned their second.

Most pairs managed to fledge at least one brood, and one pair of banded birds fledged three broods. This could only have occurred if no nests were abandoned during the breeding season (see 6.8). A pair of Yellow-breasted tits raising three broods in one season has not been previously reported. Gibb (1961), however, suspected that the Pied tit might be capable of raising three broods in a season.

6.6 NESTLING STAGE

6.6.1 Duration of nestling period

Hatching was not observed. Parkin and Parkin (1951) recorded that the three eggs of a Pied tit's nest hatched some time between

4.50 p.m. and 6.00 p.m. If incubation started with the laying of the last egg, then the eggs should hatch at about the same time.

The duration of the nestling period has been documented in the literature. Soper (1976) gave a general figure of 17 days, Oliver (1955) 19 days for a brood of four, and Anglesey (1957) 20 days for a brood of five. Parkin and Parkin (1951) gave a figure of 17 days for a brood of three, and Wilkinson and Wilkinson (1952) a general figure of 17-18 days for the Pied tit.

Because exact dates were not known for hatching and fledging for the same nests in this study, only approximate figures could be calculated. One brood of five chicks took 19 days to fledge, and all other broods observed varied between the figures given above. An average figure of 18 days was settled upon, but there may have been a significant difference between different sized broods.

6.6.2 Behaviour of adults and nestlings

Detailed observations on adult and nestling behaviour were made on nest 4 of pair D, from hatching to fledging. This was a five chick brood. Observations on four other nests at various stages of the nestling cycle gave additional information. The majority of observations for this section, however, are from pair D's nest.

The nestling period is discussed from day one to fledging and is followed through sequentially. The appearance of new behaviour patterns in the nestlings is mentioned when the context of the pattern became obvious. Therefore, these patterns may have been present before they were recognized.

Activity patterns on and about the nest are shown in Figure 6.2 a-f. The relevant figure reference is placed next to the day being discussed, with the duration of the timed observation period in brackets.

General behaviour of adults

With the appearance of the nestlings, the male no longer fed the female. Both sexes fed the nestlings, but only the female brooded them.

Day 1. Figure 6.2a (146 minutes)

During the first day after hatching the female spent 66% of her time on the nest brooding the nestlings (compared with an attentiveness figure of 72.5% during incubation). Brooding periods ranged from 2 to 50 minutes. During the longer periods on the nest the female moved about considerably; scratching her head, ruffling her feathers and preening.

She only left the nest when the male flew in to feed the nestlings. He signalled his presence beforehand with a few quiet call notes, and when he flew up she always left the nest. The female rarely stayed off for more than a few minutes at a time, and during her absence from the nest searched for food of her own and also brought back food for the nestlings. She usually settled back down on the nest after flying back. Therefore, because of the high brooding rate by the female, the male did nearly all the feeding, often returning to the nest once or twice while the female was away.

A noticeable behaviour pattern of the male when he flew up to the nest was that he sometimes remained on the rim, peering down into it. His frontal spot was very evident during these periods. He remained on the nest rim for six minutes on one occasion, and on two occasions did not leave the nest until the female had resettled on to it. Therefore, one of the adult birds was present on, or near the nest all the time except for the few minutes between when the male flew off after feeding the chicks and the return of the female.

The frequency of feeding trips to the nest was low, suggesting that the chicks required only a small amount of food to keep them satiated. Often only single prey items were brought to the nest, and

quiet begging noises were heard when they were fed to the chicks. The small amount of food required was also demonstrated when the male flew up to the nest with a small caterpillar and remained on the nest rim for four minutes, unable to dispose of it. Finally, after the female had returned to the nest and settled down, the male fed the caterpillar to her, and flew off.

Day 6. Figure 6.2b (158 minutes)

By day 6 the behaviour pattern of the female had altered. Although she was still brooding regularly, she did so only for short periods ranging from 4 to 11 minutes. Over the timed 158 minute period her brooding rate had dropped to 40%.

As on day 1 when the male arrived with food, the female flew off. On only one occasion during the entire nestling period was she seen to remain on the nest when the male flew up. This happened when she had been on the nest for one minute and instead of flying off she moved to one side while the male fed the chicks and settled back down once he had left.

When the female was brooding, the male gave a few call notes or phrases of song before flying up, and brief twitters were sometimes exchanged as she flew off the nest. When both birds flew up to the nest at the same time, one waited until the other had finished and then flew on. The female made few purely feeding trips to the nest, usually settling down on her return. The male made one to three feeding trips to the nest while she was off.

There were periods when neither parent was on the nest. These ranged between 9 and 14 minutes. The weather conditions may have affected the duration of such periods. The begging response of the chicks may also have been important. If the response was weak, then the feeding rate might drop off. Feeding rate would also be affected by the number and size of prey fed at a time.

Figure 6.2a-d

Activity pattern of pair D feeding five nestlings, over time.

for female indicates incubation.

for male indicates time spent on rim of nest on day 1.

male and female arriving at nest at same time.

• represents feeding trips to nest by either sex.

FIGURE 6.2

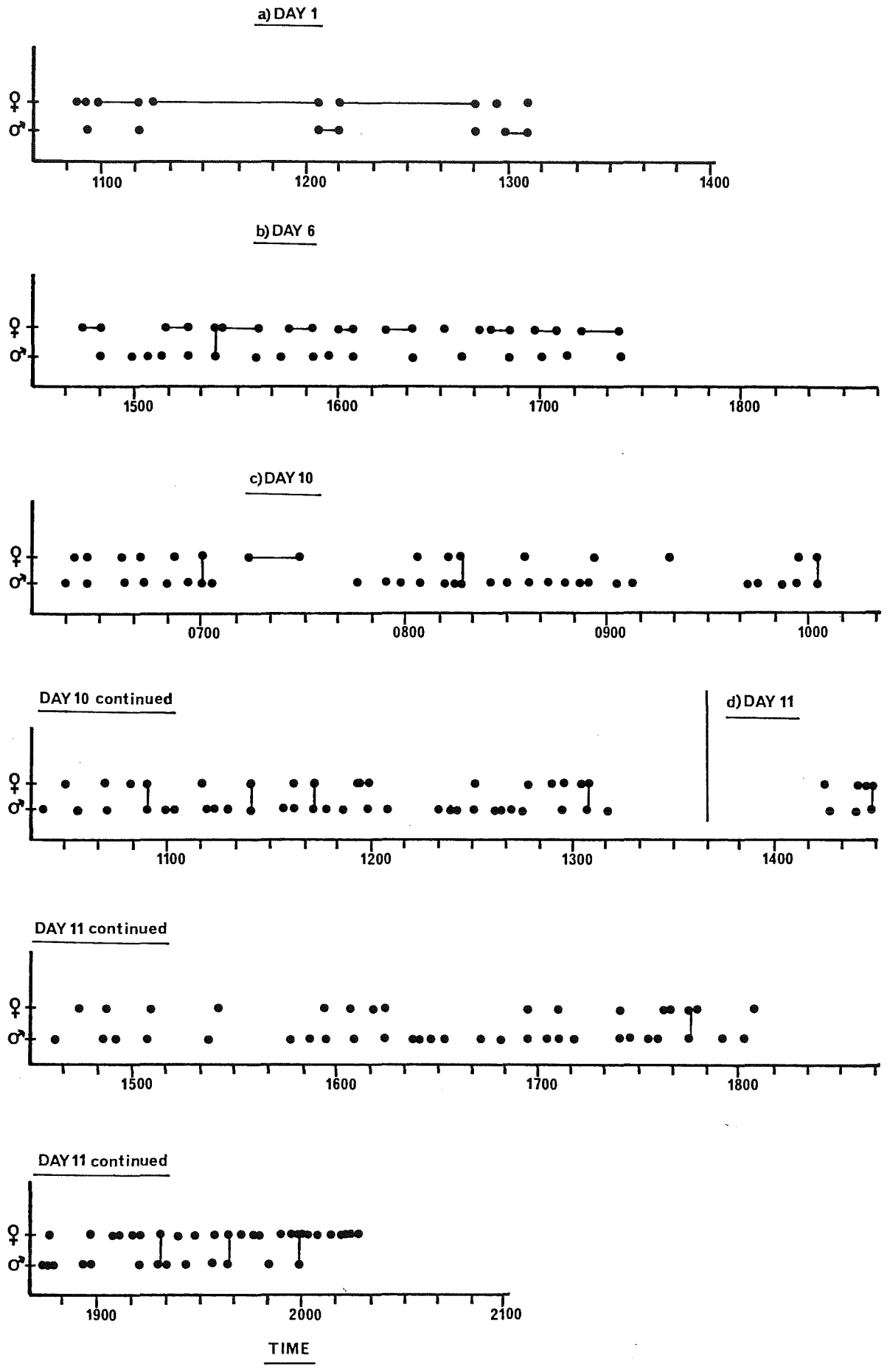

a) DAY 1
♀
♂
1100
1200
1300
1400
b) DAY 6
♀
♂
1500
1600
1700
1800
c) DAY 10
♀
♂
0700
0800
0900
1000
DAY 10 continued
d) DAY 11
♀
♂
1100
1200
1300
1400
DAY 11 continued
♀
♂
1500
1600
1700
1800
DAY 11 continued
♀
♂
1900
2000
2100
TIME

Figure 6.2 (continued) e and f.

Figure 6.3

Male and female feeding rate on days 10 and 11

▲ female

△ male

○ total

FIGURE 6.2 continued

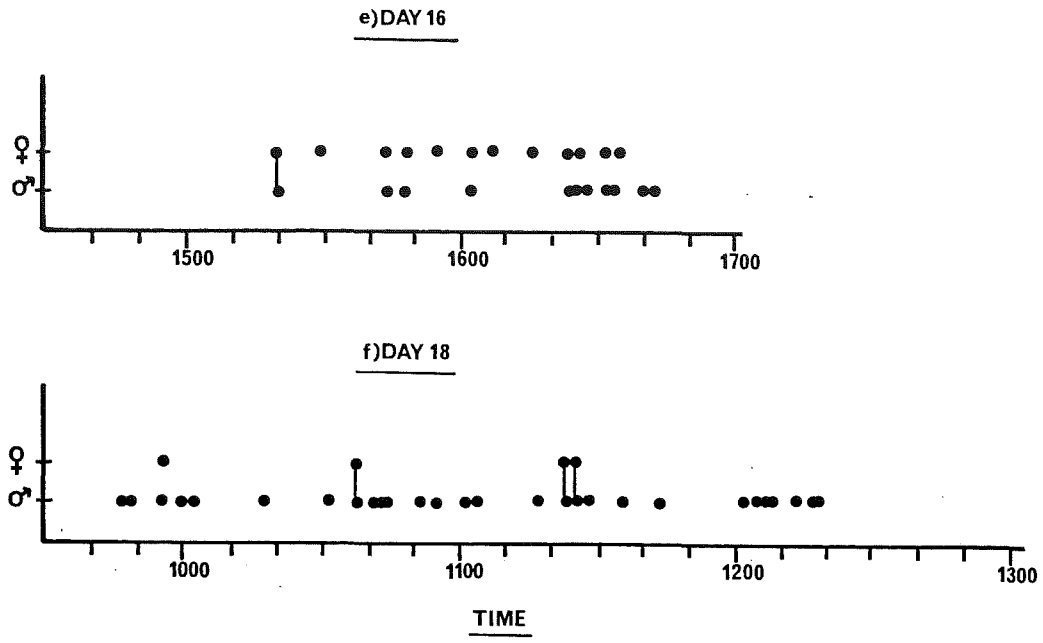
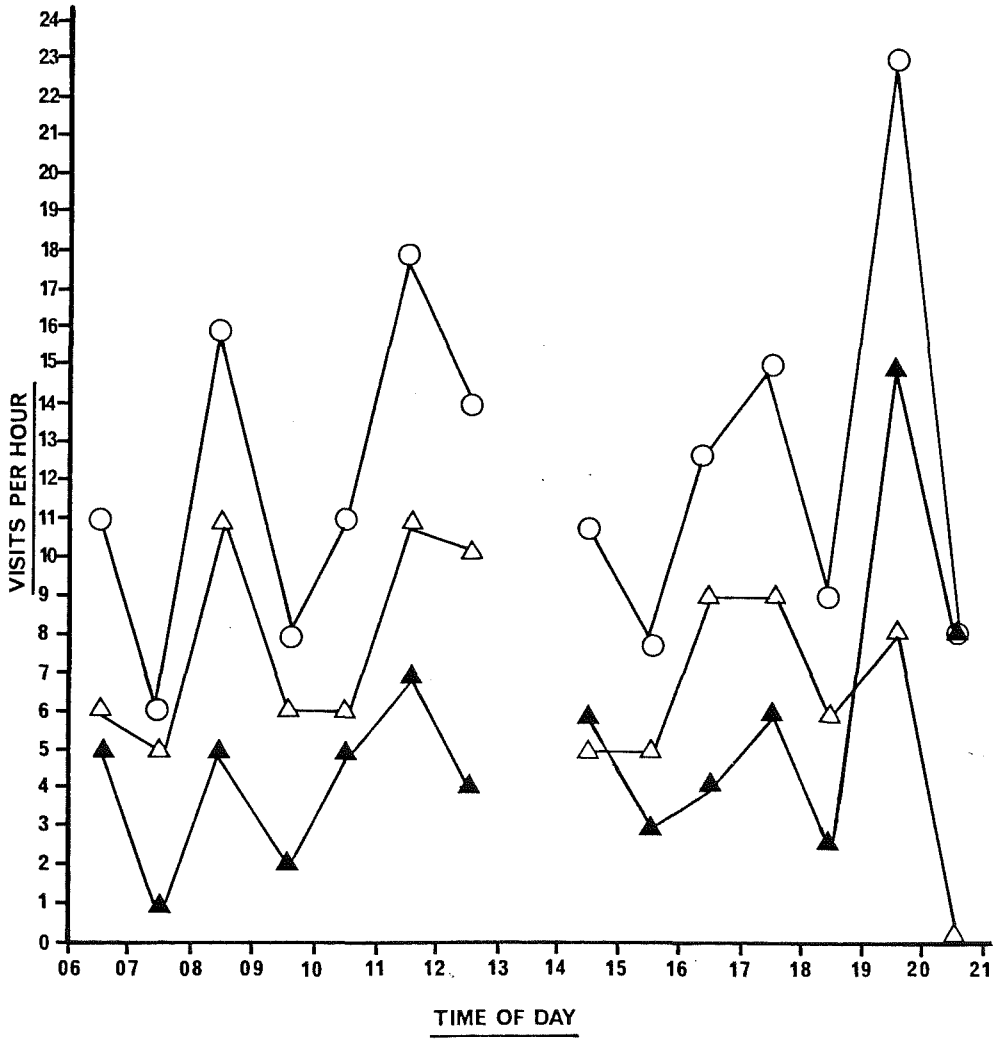


FIGURE 6.3 MALE AND FEMALE FEEDING RATE



The male had a higher feeding rate than the female. In the 158 minute period in Figure 6.2b the male made 17 feeding trips to the nest whereas the female made only three. Although she returned to the nest nine other times and resumed brooding, she did not feed the chicks on every occasion.

On some trips the adult birds flew off with faecal sacs and dropped them up to 20 m away from the nest. They usually wiped their bills vigorously against a branch immediately afterwards (see 6.6.3).

When both birds were off the nest they did not forage together, but moved about in different areas around the nest. The female foraged closer to the nest than the male. When the chicks were fed, begging noises were heard and gaping beaks seen. (According to Soper (1976) the nestling's eyes opened around this date.)

The nest area was carefully watched by the parent birds when searching for food. On one occasion the male chased away an intruding male tit which had landed in the nest tree. The defending male sang briefly afterwards.

Days 10 and 11. Figure 6.2c (410 minutes) and Figure 6.2d (365 minutes)

By this time brooding had virtually ceased. The female was seen brooding only once on day 10, for a period of 14 minutes. This was early in the morning before the sun had reached the nest area.

Both adult birds were feeding the chicks regularly and only approached the nest for this purpose. The male was more vocal than the female when approaching the nest, giving call notes and phrases of song whereas she was usually silent or gave only a few quiet call notes. More rarely she sang a few quiet song phrases when arriving and leaving. (This has also been observed for the female Pied tit (Wilkinson and Wilkinson, 1952).) The majority of the female's trips to the nest were only noted with continuous observation on the nest.

When gathering food the male called and sang subsong and full song, and less commonly remained silent. The female remained quiet apart from countercalling with the male at irregular intervals. Quiet begging calls were given by the chicks when fed but they did not beg on every feeding. Begging sometimes continued for a few seconds after the parent had left the nest. The duration of the begging may indicate how hungry the nestlings are.

The parent birds always approached the nest from below, moving upwards from perch to perch until the level of the nest was reached. The only occasion on which the nest was entered from above was when dusk approached. The light level dropped considerably in the bush over this period so that entrance and exit were easier from above.

Interactions between a pair were rare while feeding was in progress. On one occasion the female begged briefly as she flew up to the nest and as the male left. He ignored her. On another occasion the male displayed his wings horizontally to the female as he left the nest and as she flew up.

Feeding rates of adult birds over days 10 and 11

Although both birds fed the chicks, their feeding rates differed. Figure 6.3 shows the number of trips made to the nest per hour by the male and female during days 10 and 11. Observations were made on day 10 for a 410 minute period (from 0620 hrs) and on day 11 for a 365 minute period (from 1415 hrs). The figures given before 0700, between 1400 and 1500 and after 2000 hours are for parts of an hour only. No observations were made between 1310 and 1415 hours.

The male feeding rate was higher, or similar to, the female rate for all periods except after 2000 hours. Why a difference in feeding rates existed could not be explained as the female was often observed around the nest tree but did not fly up to the nest as regularly as the male. The male rate varied from 0 to 11 trips per hour whereas the

female rate varied between 1 and 15 trips per hour. The feeding rate varied considerably over the day, with no distinct pattern. A large increase in the rate occurred in the hour before darkness, however, with the female doing all the feeding after 2000 hours.

The interval between feeding trips varied considerably for both sexes (see Table 6.4).

Table 6.4. Time between feeding trips for each sex on days 10 and 11.

		Range (mins)	Mean	Variance	n (sample size)
Day 10	Male	1.0 - 44.0	7.1	52.4	56
	Female	0.5 - 36.0	12.5	94.0	31
Day 11	Male	1.0 - 42.0	8.3	51.2	42
	Female	0.5 - 45.0	8.2	100.3	44

On day 10 the female averaged a longer time between visits than the male. Her visiting rate was also more variable. On day 11 the mean rate of both sexes was the same, but this was due to the increase in the female feeding rate towards dusk (as shown by the high variance). The male feeding rate was similar over the two days.

Day 14

No brooding was observed. The nestlings were well-feathered and very active. Occasional wing fluttering and jostling about were observed after the parent bird had left the nest. The bright orange-red gapes of the nestlings were very evident. Adult feeding behaviour was similar to that of days 10 and 11 with up to 10 minutes between trips to the nest.

Day 16. Figure 6.2e (82 minutes)

The streaking on the heads of the nestlings was very noticeable. Their heads were thrust up immediately when a parent arrived at the nest. After it had left, the begging calls continued for up to 5 seconds,

after which time the nestlings huddled down so that they were difficult to see over the nest rim.

The adult birds often waited for the appearance of a faecal sac before flying off. The feeding pattern was as observed over earlier days.

Day 18. Figure 6.2f (150 minutes)

As the male approached the nest each time, he called and sang loudly. The nestlings began giving out loud begging calls when he was within 8-10 m of the nest, and when he flew up to the nest to feed them they moved about and fluttered their wings. The most noticeable behaviour pattern over the 150 minute timed observation period was the differential feeding rate of the parent birds. Whereas the male made 28 trips to the nest over this period, the female made only four. Although she was seen regularly about the nest tree she did not approach the nest. The reason for the female's low feeding rate was not established.

Summary

The behaviour patterns of the parent birds changed as the nestlings became older. From a high brooding rate during the first few days after hatching, the rate steadily dropped so that by about day 10 little or no brooding took place. The male's feeding rate was higher than the female's rate throughout the nestling period. In addition, his visits to the nest were more regular than hers.

6.6.3 Faecal sacs

Urine and faeces in nestling passerines are voided encapsulated in a structure called the faecal sac (Morton, 1979).

During the first three or four days of the nestling phase the parent birds did not remove the faecal sacs. Therefore, they must have eaten them as they were produced. This is a feature common to

many species of passerines (Morton, *op. cit.*).

By about the fifth day, however, the adults regularly removed the sacs and dumped them within 20 m of the nest.

Faecal sacs were not allowed to accumulate in the nest and were removed as soon as they were produced. On several occasions a nestling was seen to present its rear to a waiting adult and excrete a faecal sac, which was immediately removed by the adult. Faecal sacs were not produced (and hence removed) after every feeding visit to the nest.

During the last two days of the nestling phase, the pattern of removal changed. Nest hygiene deteriorated and sacs collected on the rim of the nest after being deposited there by the nestlings. Sacs were sometimes removed by the adults. The accumulation of faecal sacs indicated that the nestlings were close to fledging. They also collected on the ground below the nest.

6.6.4 Duration of feeding trips to the nest

When a parent flew up to the nest, it was only to feed the nestlings (apart from brooding by the female over the first few days). The adult remained on the nest only long enough to feed the prey to a nestling and perhaps remove a faecal sac. Longer periods on the nest resulted from the adult waiting for the production of a faecal sac.

Table 6.5 shows the length of time spent on the nest by each parent, at different periods of the nestling phase. Both sexes spent similar lengths of time on the nest.

Table 6.5. Duration of feeding trips to the nest.

Day	Sex	n (sample size)	Range (secs)	Mean (secs)	Variance
6	Male	17	2.0 - 30.0	9.5	48.8
	Female	(8)	-	-	-
10	Male	51	3.0 - 30.0	9.8	14.7
	Female	24	3.0 - 20.0	9.5	13.5
11	Male	30	2.0 - 15.0	8.7	6.8
	Female	31	4.7 - 25.0	11.4	28.4

- indicates that the female returned to the nest and began brooding.

6.7 DEPENDENT FLEDGLING STAGE

6.7.1 Fledging

Fledging was not observed. Parkin and Parkin (1951), Wilkinson and Wilkinson (1952) and Soper (1976) recorded examples in which once the chicks had left the nest, they did not return, and once one chick had fledged the others quickly followed. Best (1975), however, found that young Black tits took several hours to leave the nest permanently. They often began by following a parent off the nest after a feeding visit, and then returning. This would occur several times at the end of feeding visits before they finally ceased to return.

As the nestlings approached fledging they were liable to explode off the nest if disturbed by an intruder. This happened for one nest which I found. When I put my hand into the nest to capture them for banding, the three nestlings quickly scattered away from the nest. The male, however, on flying back to the nest with food and finding it empty, immediately began calling. The chicks answered with begging calls and after 20 minutes the male had them within a few metres of each other and continued to feed them.

6.7.2 Number of chicks fledged per brood

Observations were made on fourteen broods of fledged chicks. Twelve of these were of four chicks, and one each of three and five.

Survival rate to independence appeared to be 100%.

6.7.3 Fledgling and adult behaviour

This section covers the behaviour of the adult birds and the behavioural development of the fledglings through to independence. Figure 6.4 summarizes the first identifiable appearance of behaviour patterns in fledglings.

The results are based on the observations taken from five broods of known age, and supplemented with data from other broods for which the exact ages were not known. Development is followed through chronologically and where a behaviour pattern is first mentioned, this is when it first became obvious. Calls mentioned in this section are discussed in Chapter 9.

Day 1

After fledging, the chicks could be found within a few metres of the nest site. They stayed high in the vegetation, usually just under the canopy - from 5 m up to 10 m high. A similar behaviour pattern has been observed in newly fledged Pied tits (Wilkinson and Wilkinson, 1952) and Black tits (Best, 1975). Such behaviour may have been a safety device which only became less necessary on the development of the fledglings' flying abilities. Because of the behaviour of the chicks, the parent birds searched for more food in the sub-canopy than they would have normally.

The chicks' tails were very short, their gape prominent and their flying abilities clumsy. Two or more chicks characteristically huddled together for periods ranging between 2 and 45 minutes (Figure 6.4a).

FIGURE 6.4 FIRST APPEARANCE OF BEHAVIOURAL PATTERNS IN DEPENDENT FLEDGLINGS

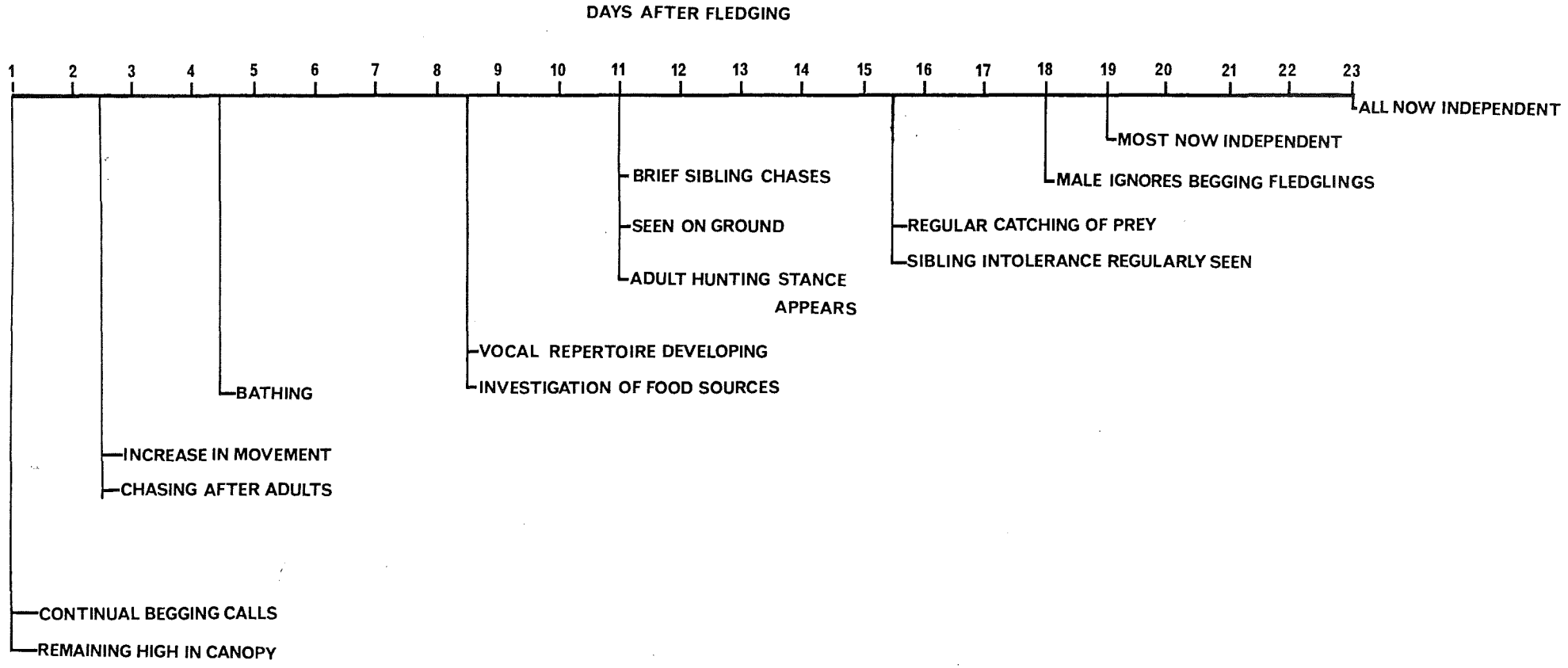


Figure 6.4a. Newly fledged chicks

Almost continual begging calls were given whether the parent birds were present or not. Adult birds were not actively pursued for food, but the chicks did give a flying-chrup call when flying about. When by themselves they remained immobile for a few minutes before flying to another perch. As a result of this indiscriminate flying about they became widely scattered, but the adult birds called until they had gathered the chicks up again.

Both parent birds fed the chicks, often feeding an individual or a group of chicks four or five times in a row before shifting their attention to the others. Because of the almost continual begging calls, the adult birds gave few calls when coming in to feed the chicks. When the chicks became silent, however, the parent birds emitted a few call notes which elicited an immediate begging response from them. Call notes, therefore, acted as a location call so the adults knew where the chicks were and also alerted the chicks that they were going to be fed. On one occasion, a male returned to a branch to feed a young female who had flown to another branch while he was gathering food. On discovering her absence he gave loud call notes and a few phrases of song to which the chick reacted immediately with begging calls. Intervals between feedings ranged from a few seconds up to 10 minutes.

Days 2-3

If the female is going to renest she will do so over this period. As she no longer assists in feeding the chicks, the male continues to feed all of them. However, if renesting does not take place, the female continues to assist with the feeding.

During days 2 and 3 the chicks became more agile and moved about with their parents throughout the territory. Some chicks were seen within 3 m of the ground.

Begging calls were still given almost continuously but the chicks

also chased after the adult birds, in an attempt to solicit food. Periods of rapid movement alternated with periods in which the chicks remained in one place. On one occasion, two chicks remained huddled together for 105 minutes without being fed by a parent.

As soon as an adult bird was seen a begging posture was assumed, with the head thrust forward, gaping beak and ruffled wings. This reaction resulted even if the parent had an empty beak. The presence of another tit nearby appeared to be of sufficient stimulus to cause the begging reaction. Food was always poked into the gaping beak of a chick by the parent.

Even when the chicks were silent the parent bird returned to the same place several times in a row to feed them, and when they were not begging for food, two or three chicks huddled together with their eyes closed.

Possible investigation of food sources was seen. Once, a chick pecked at a branch six or seven times as if trying to catch a prey item. No searching behaviour in the adult manner was seen.

One chick was heard burbling briefly but the only common calls were the begging calls when immobile, and the flying-chrup call when flying about. Chrup calls were given irregularly by chicks of all broods when they were not begging for food.

Days 4 to 7

Behaviour during days 4 to 7 was similar to that for the previous period. However, by this time the chicks had become very agile and pursued the parent birds whenever they saw them. Again, periods of rapid movement alternated with periods of no movement (up to 60 minutes in one example). Male D and his five chicks were seen trespassing on their neighbour's territory, but were not challenged by him (see Figure 4.7c).

On day 5, fledglings were observed bathing in a shallow stream, for the first time. Pecking at branches did not appear to be associated with prey capture.

Over this period the frequency of begging calls dropped off, with fewer calls being given while the parent birds were absent. This resulted in the adult birds giving more calls before they came in with food. Some food items were swallowed with difficulty. In one incident the adult male captured a blowfly and placed it in the open beak of a begging chick who was unable to swallow it, and dropped it. The male immediately flew to the ground from 6 m away, retrieved it and offered it to another chick who was also unable to swallow it. He removed it from the chick's beak and passed it to a third begging chick with the same result. Finally a fourth chick managed to swallow it. When a male was feeding the complete brood, he fed two or three chicks several times in a row and then shifted to the others which may have been up to 50 m away.

When silvereyes, grey warblers and intruding tits approached the chicks too closely the male chased them away.

Days 8 - 9

By this time the chicks were as agile as the adults and moved about at all levels of the vegetation, but not on the litter layer. Their tails were fully grown.

The first positive signs of investigation of possible food sources were seen during days 8 and 9. Searching was not carried out in the usual tit manner however, which involved scanning an area from a stationary point. Instead they moved through the vegetation, half-clambering, half-flying, pecking at leaves and branches. The bark and knotholes of fuchsias were also inspected. One young female was seen pulling pieces of moss from a branch and mandibulating them.

Very little appeared to be caught during these activities.

Rapid pursuit of the adult birds when seen also dropped off. Instead the chicks began to fly over to the parent to be fed. Cases of mistaken identity also occurred. For example, a young female begged off an independent juvenile male which landed nearby.

Vocal abilities also showed development over this period. In addition to the chrup, flying-chrup and begging calls given by both sexes, young males were heard singing juvenile song and staccato chucks were given by a young male at a young female.

Days 10 to 12

Behavioural patterns observed during days 8 and 9 continued to develop. More juvenile song, and call notes similar to those given by adults, were heard. Staccato chucks, given in aggressive situations, were also heard more commonly. Fewer begging calls were given by the fledglings as they flew about, and the frequency of chrup calls also decreased. Cases of mistaken identity were still seen. In one example, a young male flew up to a young female and gave the begging posture and calls seen when being fed by a parent. Brief chases in which males chased females were seen intermittently.

Chicks were first seen on the ground hunting for food over this period. The usual hunting stance was used (see Chapter 8). Hawking was also seen. In one example a male flew up and attempted to capture a moth flying by, but missed. He repeated this action and missed again. His actions were poorly coordinated.

Periods of inactivity became fewer and chicks remained huddled together for only a few minutes at a time.

Days 13-14

Begging calls were elicited when an adult bird was seen, when it approached the chicks, or in answer to calls from an adult bird.

Otherwise, the fledglings usually remained silent.

Parent birds were still rapidly pursued by loudly begging chicks, which fluttered either one wing or both wings when on a branch. Periods of silence with no pursuit were interspersed with chasing and loud begging calls. The parents could, however, approach the chicks without them chasing after them. Chicks still huddled together when not demanding food.

Although food sources were commonly investigated, prey items were seldom caught. Some chicks still fluttered through the vegetation pecking at leaves and branches.

Days 15-16

Active searching for, and the regular catching of, prey items from branches, leaves and the litter layer were seen. The fledglings moved through all the vegetation levels up to about 10 m, and flew to the ground regularly. The usual hunting stance was commonly seen and prey items were taken as they were seen. However, whenever a parent bird was seen they still begged for, and received, food and probably obtained most of their food from the adults. Begging calls were given only when an adult was seen or heard. They seldom chased after the adult bird.

Young males and females sang juvenile song and subsong regularly, and on one occasion a young male flew up to his brother who was singing and gave the begging posture and calls.

Sibling intolerance became very evident over this period, being most noticeable between brothers. For example, two brothers were seen chasing each other. They then resumed searching for food side by side and then two minutes later began chasing each other again.

This was the first time at which the fledglings approached me. They remained still, silent and staring for up to about one minute.

Day 17

Fledglings spent more time searching for food by themselves but were still fed regularly by the parent birds.

Day 18

By this time fledglings moved about independently of their parents, searching for, and catching prey regularly, but not all attempts at catching prey were successful. For example, a male chased a prey item down a branch, dabbed at it three times but missed on each attempt. Trunks, branches, leaves and the litter layer were all inspected.

Very rarely, two chicks huddled together on a branch, usually for no more than 5 to 10 minutes. Vocal abilities continued to develop with begging noises, burbling, call notes, song and chatter between chicks being heard.

The following extracts from my notebook for male D and his five fledglings illustrate the main events occurring on day 18:

Male D was seen searching for food. Two fledglings (a male and female) began begging loudly when they saw him and flew over to him, but he ignored them. He flew down to the stream-bed, possibly with the intention of bathing, but the still-begging fledglings followed him down. After he flew off without feeding them, the fledglings became silent and began searching for food about 30 cm above the ground, i.e. once the stimulus of the male had gone they resumed searching for food. They caught several prey items. The young male then had a bath in the stream, dipping his head into the water, and crouching down and fluttering his wings.

About 15 minutes later, male D let out a loud call note near where the fledglings were still searching for food. They responded immediately with begging calls and chased after him. However, he still did not feed them. After 45 minutes he finally began feeding them, but

although they pursued him constantly, he fed them only intermittently. Between feedings they searched for their own food. Despite their reaction to the presence of the male, however, they did not pursue him every time he appeared near them. When he was feeding the fledglings the male returned to where he had fed them the previous time, even if they were not calling or had moved away. On occasions the other fledglings from the same brood approached the male but did not beg from him. These birds appeared to be independent, or close to it, and were promptly chased away by him. Begging chicks were either fed or ignored, but never chased. When independent fledglings approached begging fledglings, they took little notice of them.

Near-independent birds also gave begging calls amongst the feeding chatter and juvenile song as they moved about searching for food.

Aggressive interactions were commonly seen between siblings, particularly between brothers, and brother and sister, and took the form of chases and fighting on the ground with claws entangled. Bill clicks were also given.

Days 19-20

By the 19th day many broods were independent, i.e. they were no longer fed by the parents and did not react to their presence when they saw them.

The behaviour of those fledglings still being fed was similar to that observed for day 18, in that they continued to feed by themselves until they heard an adult call. They immediately replied with begging calls and were sometimes fed.

Although male D was feeding only two of his five fledglings on day 18, he was seen feeding at least three over days 19-20. Therefore he may have fed the other members of the brood only if they gave the begging response. Periods of continuous feeding by the male alternated with periods where no feeding was done. Two female chicks huddled

together for 15 minutes on day 20. Otherwise all fledglings moved about independently.

The one or two chicks of a brood of four or five which were fed over this period may have been less advanced than their siblings. This may have arisen if the eggs did not hatch at the same time.

Days 21-22

By this time, the one or two individuals of a brood which had been fed by the adult birds over the previous few days were obtaining all their food as they moved about. They sometimes reacted to an adult call with a begging call, but were rarely fed.

Independent juveniles moved about by themselves and did not react to the calls given by the adult birds.

All fledglings were independent after this period.

6.7.4 General comments

When both parents fed a brood they often fed certain chicks exclusively. This happened when fledglings became separated through their general movements and one parent stayed with them and fed them. However, the chicks fed by a parent changed if they all met up and then separated into different combinations. Similar behaviour has been noted in the Pied tit (Wilkinson and Wilkinson, 1952). Often the adult birds moved about in different parts of their territory with their charges. Final broods of the season may have been fed longer than broods fledged earlier in the season.

Over the dependent fledgling stage there was a gradual change in the reaction of fledglings towards the adult birds. Initially the chicks begged almost continuously whether the adults were present or not. Gradually, however, they only reacted when the adult called or moved near them. Finally, just before dependence they showed a variable response to their presence and calls.

The response to the calls or presence of an adult bird appeared to be innate. This was demonstrated by near-independent fledglings which were capable of finding their own food. They often begged off the adults when they called or appeared, but resumed feeding on their disappearance. This reaction disappeared on independence.

6.7.5 The transition to independence

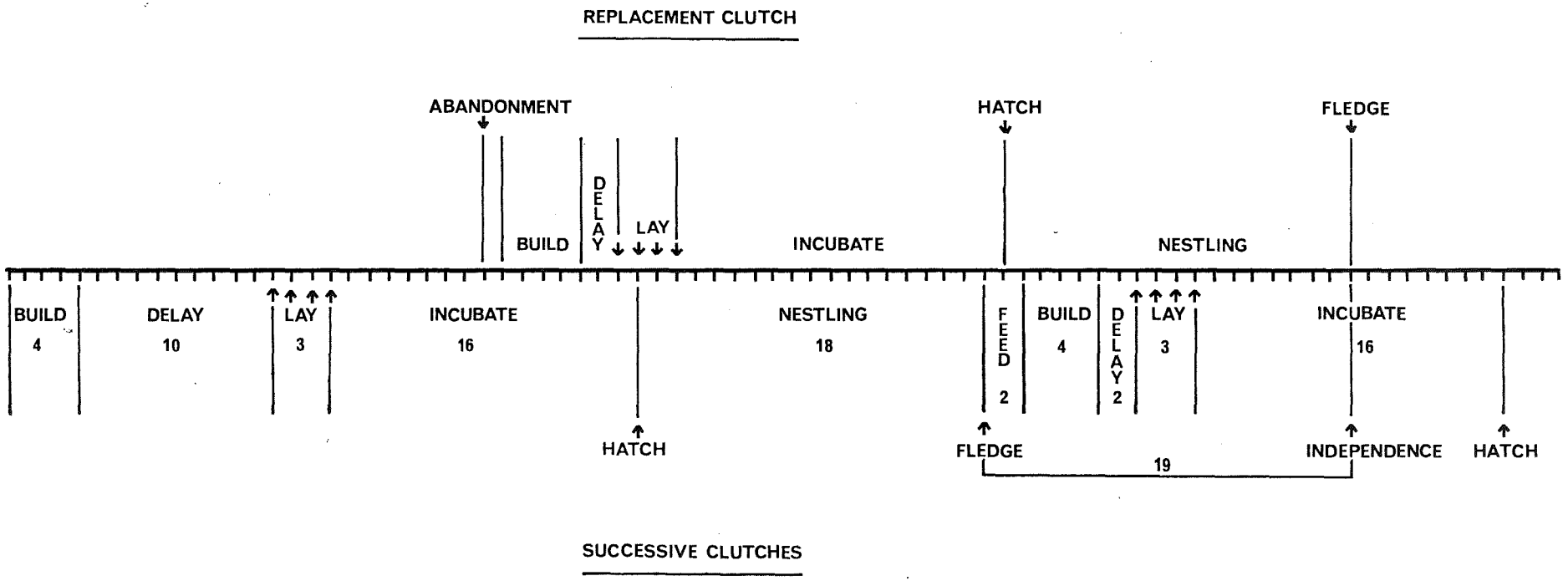
Davies (1978) envisaged two extremes in the process of transition to offspring independence. Either, as they got older, the young became progressively better at looking after themselves, and in response the parental investment decreased accordingly, or the parents initiated the process by progressively reducing their investment and thereby forced the offspring to look after themselves.

For the fledgling Yellow-breasted tits the transition to independence appeared to be a mixture of these two extremes. Fledglings searching for food were seen regularly from about day 15 onwards, with the majority of the young achieving the transition to independence by becoming more adept at catching their own prey, and hence demanding less from their parents.

Some fledglings, however, continually demanded food when they saw an adult. These birds may have been less advanced than their siblings. This resulted in the adult refusing to feed them for long periods, during which time the fledglings searched for their own food. After a few days they reacted less vigorously to the presence of the adults and finally, ignored them on independence.

The first method of transition was more commonly observed than the second.

FIGURE 6.5 THE BREEDING CYCLE OF THE YELLOW-BREASTED TIT



6.8 CONCLUSION

The breeding cycle of the Yellow-breasted tit is summarized in Figure 6.5, for an average four egg clutch. The average duration (in days) of each part of the cycle is also indicated. The delay caused by nest abandonment is shown by the replacement clutch after eight days incubation of the original clutch. The sequence of events when renesting after a successful fledging is also shown.

The time from the laying of the first egg to the fledging of the nestlings was 37 days. To compare this figure with those provided by Nice (1957) for Northern Hemisphere passerines, a further day has to be added as she allowed an extra day for laying. For hole-nesters in Europe and the U.S.A. the cycle took 38 days, the same for the Yellow-breasted tit, which nested in cavities and positions sheltered from above. The cycle for open-nesting birds took 31.4 days in Europe and 27 days in the U.S.A. Clutch size and incubation period however, differed from the tits in that the hole-nesters had a larger clutch size and a shorter incubation period. Gill (1979) gave a figure of 43.7 days for the Grey Warbler.

From the length of the breeding cycle the theoretical number of broods possible per breeding season can be calculated. To find the time to fledge the second brood, a further two days must be allowed for the female to feed the fledglings, four for rebuilding and two for the delay until the first egg is laid (= 8 days). Therefore the time required to produce the second brood = 45 days. One pair produced three broods, so a further 45 days must be added. The time to build the first nest and the delay before laying was 14 days, and the time for the last brood to become independent was 19 days. Therefore the time required to produce three broods was 14 + 37 + 45 + 45 + 19 = 160 days.

The time available for breeding can be found by determining the time between when breeding activities were first observed (i.e. nest

building) and when the last brood became independent. The earliest breeding date observed was 7 September, and the latest was 24 February = 171 days.

Therefore a maximum of three broods can be produced in the time available. This would only be possible if no nests were lost during the breeding season. Nest abandonment usually occurred part-way through incubation, so that in the example on Figure 6.5, 25 days of the cycle would be required to reach the same stage at which nest abandonment occurred, for the replacement nest.

Although the last brood was independent by the end of February in the study area, Nest Record card 6456 for the Pied tit records a brood of two about to fledge on 21 February in Kaingaroa State Forest. The fate of the brood was not determined, however.

Table 6.6 summarizes the breeding cycle of other members of the genus *Petroica* within the New Zealand region. The Pied tit probably has the same cycle as the Yellow-breasted tit. All figures are averages.

Petroicas resident on islands tend to breed later and have fewer broods than their counterparts on the mainland. For example, the Snares Black tit probably has only one brood per season, starting during November. South Island robins on Outer Chetwode Island have fewer clutches and breed later (Flack, in prep., b).

Table 6.6. Comparison of the breeding cycle of the Yellow-breasted tit with other members of the genus

Species	No. of broods	Time to complete nest	Delay before laying	Clutch size	Incubation period	Nestling period	Fledgling period	Source
Yellow-breasted tit	up to 3	4	7-11	3-6	16	17-20	18-23	This study and references in text.
Snares Island Black tit	1	3-6	2-7	2-3	20	17-22	21-28	Stead, 1948; Best, 1975; Nest Record Cards 11569-72
South Island robin	up to 4	1-4	5-7	2-4	17½-18	20-24	30-49	Flack, 1973, in prep. b; R. Powlesland, pers. comm.

All times in days.

CHAPTER 7

PLUMAGE AND MOULT

7.1 INTRODUCTION

The adult and juvenile plumages of the Yellow-breasted tit have been described in detail by Fleming (1950) and Oliver (1955), although Fleming's descriptions are based primarily on museum skins.

The timing and sequence of the moult are less well known. There is one moult a year, with adult birds having completed their moult by May. Birds in juvenile plumage are present only between November and February (Fleming, *op. cit.*).

This chapter is divided into two sections. The first part briefly compares the juvenile and adult plumages for each sex and also discusses the eye ring, a characteristic not mentioned in the literature, although it is plainly visible in photographs of females in Fleming (*op. cit.*) and Soper (1976). The second part discusses the moult of birds in juvenile plumage and the post-breeding season moult of the adult birds.

The results for this chapter are based on birds handled during the study, and observations made on banded and unbanded birds throughout the year. The number of birds captured in each plumage category (including recaptures) was as follows: adult male 11, adult female 16, juvenile male 9, and juvenile female 5.

7.2 PLUMAGE

Adult and juvenile plumages for both sexes are very distinctive. Tables 7.1 and 7.2 compare the differences between the plumages for each sex.

Table 7.1. A comparison between males in adult and juvenile plumage.

Feature	Adult	Juvenile
Dorsal plumage	Glossy black	Head, nape and rump dull black, each feather with a pale yellow shaft.
Ventral plumage	The black continues under the chin to a distinct division with the yellow on the breast. Flanks are of a paler yellow with occasional black streaks.	The black continues under the chin, where there is an uneven division with the yellow on the breast. The yellow is dull and usually heavily streaked with black. Flanks are yellow with black streaking. Plumage as a whole is much duller than adult plumage.
Frontal spot	Vivid white and crescent shaped.	Small and insignificant. White in colour but covered by black-tipped feathers. Rarely visible.
Eye ring	A non-contrasting ring of bare black skin.	Usually as in birds in adult plumage, but sometimes a few small white feathers form an incomplete circle around the eye.

Table 7.2. A comparison between females in adult and juvenile plumage.

Feature	Adult	Juvenile
Dorsal plumage	Soft brown, under-laid with grey.	Head, nape and rump brown with a pale yellow shaft to each feather.
Ventral plumage	Pale to bright yellow up to the chin, merging into brown and then white, over-laid with brown-tipped feathers under the chin. Flanks yellow, streaked with brown. Depth of yellow and amount of brown streaking on the breast and flanks varies.	Pale yellow, often heavily streaked with brown, up to the chin. A mixture of brown and yellow feathers under the chin. Flanks heavily streaked with brown. Appearance duller than females in adult plumage.
Frontal spot	Occasional birds have a vivid white, crescent-shaped spot as in males, but size varies considerably.	Small and insignificant. Pale white in colour, heavily overlaid with brown-tipped feathers. Rarely visible.

Birds in adult male plumage are shown in the frontispiece and Figure 4.10. The heavily moulting male in Figure 7.3 is in near-adult plumage. A comparison between these males demonstrates the variability in the breast colouration. In birds in adult plumage, the yellow fades during the year so that the original deep yellow has often faded to a much paler shade by the end of the breeding season. On some birds there is an orange band 1-2 mm wide at the breast division. This was also noted by Poole (1951).

Males in juvenile plumage (Figures 7.1 and 7.2) have varying amounts of black streaking on the pale yellow of their breasts. Faint head streaking is visible in Figure 7.1 and the frontal spot is visible on the bird in Figure 7.2.

Figure 7.6 shows a female in newly moulted plumage, caught in a mist net. Note the flecking about the eye and pale breast colour.

Females in juvenile plumage are shown in Figures 7.4 and 7.5. Note the faint head streaking on both birds and the variability in the breast streaking. Both birds show the eye ring and the flecking about it. The female in Figure 7.4 shows the typical tit stance of wings held below the tail.

The wing flashes of males are white whereas those of the female are yellowish-brown.

The eye ring is prominent in females in adult and juvenile plumage, being composed of a ring of small creamy feathers about 1 mm wide, edging the bare black skin of the eyelid. A feathered eye ring is not present in males, although two out of eight males captured in juvenile plumage had a few small white feathers scattered about the eye. These were lost in the juvenile moult, so that older males had only a ring of bare black skin which was not visible against the black feathers on the head.

Figure 7.1

Male in juvenile plumage. Note the relatively streak-free breast.

Figure 7.2

Male in juvenile plumage. Note the heavily streaked breast.

Figure 7.3

Juvenile male part-way through the moult.

Figure 7.4

Female in juvenile plumage.

Figure 7.5

Female in juvenile plumage.

Figure 7.6

Female in newly acquired adult plumage.

The eye ring of the female may serve in sexual recognition (see also Chapter 4, 4.16).

7.3 MOULT

Moulting occurred once a year, starting during the latter part of the breeding season for juvenile birds, and after breeding activities had finished for the adult birds.

Although the timing and duration of the moult, particularly for juvenile birds, was determined approximately, the moult sequence was investigated only superficially because of the small number of moulting birds captured. Observations on birds in adult and juvenile plumage as they moved about revealed that the commencement of the moult could not be determined, as when these birds were captured, sheathed feathers were found hidden under the longer body feathers.

Where primary flight feathers are mentioned, their numbering is from 1 to 10, from the innermost primary to the outermost (as in Heather, 1966; and Welty, 1975).

7.3.1 Adult moult

No moulting birds were observed before breeding activities finished, and because final broods became independent at differnt times, some pairs could be moulting while others were still feeding dependent fledglings.

All birds, however, once they began to moult, became retiring and were extremely difficult to locate. They remained very quiet, and the males displayed no reaction towards taped songs played in their territory. This resulted in few observations being made on the progress of the moult.

The earliest date on which moulting was observed was on 24-1-79 in female 133. Her last brood had become independent about 10 days

beforehand. She had a short tail and a fluffed appearance and moved about quietly searching for food. When resighted on 12-4-79 there was no sign of moult.

By the 10-3-78 male 113 was moulting heavily having fed the last brood until about the 20-2-78. When recaptured on 12-3-78 the following description was obtained: tail frayed and worn, being 76% of its original length; yellow on the breast in dark and light patches; the frontal spot patchy with some white feathers missing, and scattered sheathed feathers appearing; primary 7 on both wings regrowing. Unfortunately this male was not seen again.

Up to three primaries were replaced at one time. Female 111, recaptured on 8-2-79, had half-grown primaries 2, 3 and 4 on both wings. She displayed no other signs of moult. Because the tail feathers were worn at the tips she may have just started to moult. When recaptured the year before on 6-4-78 she was in newly moulted plumage.

Adult moult therefore involved the replacement of all feathers, i.e. it was a full moult. Visible moult, in which body feathers were being replaced, was observed about 10 days after breeding activities had ceased, so sheathed feathers may have started developing at about the time of completion of breeding activities. Primary flight feathers were replaced from the innermost to the outermost.

Moulting birds were observed between late January and late March, although some birds may have been moulting after this time (particularly if they did not finish breeding activities until late February). The moult probably took less than three months.

7.3.2 Juvenile moult

The first moult which birds in juvenile plumage went through after fledging was a partial moult in which only the body feathers were replaced. This is a feature common to many species of birds (Wallace

and Mahon, 1975). The retrices and remiges were probably replaced during the moult after the bird's first breeding season.

Once the moult was completed the birds were indistinguishable from birds which had been through a full moult. However, juveniles which moulted during the end of the breeding season could be distinguished from late-breeding adult birds by the brightness of their yellow breast colour. This was particularly evident for the males. Immature males (juvenile birds which have moulted) did not have the orange breast band sometimes seen in older birds.

Figure 7.3 shows a juvenile male part-way through the moult. Note the patchy appearance of the breast colour, missing head feathers, and the ragged frontal spot. The untidy appearance is characteristic.

The breast and belly feathers completed replacement before those of the head. This was more easily seen in the males than the females because of the greater contrast between the black and the yellow in the males. Several males were seen in which the yellow of the breast was deep and even and free of black streaking whereas bald patches were often seen amongst the new glossy black feathers, sheathed feathers and the juvenile yellow-shafted feathers of the head. The most obvious sign of moult in the females that could be detected without handling the birds was the unevenness of the breast colour.

Juvenile birds began their moult earlier than adult birds, and some had completed their moult just as the adults were starting. Moulting juveniles were first seen in mid-January. If an estimated time of about two weeks is allowed for the sheathed feathers to become visible, this means that the moult began about 7-9 weeks after the birds fledged (early in November) and may have coincided with the first outward movement of some juveniles from adult territories.

The latest date in 1978 on which a moulting bird was observed was 28-3-78, while in 1979 the latest date was 6-4-79 when a male

in slightly ragged, but near-adult plumage was seen. The latest date on which a bird in full juvenile plumage was seen was 11-3-78.

Birds fledged from the second broods in late December - early January probably began moulting about late February, whereas those from later broods, fledged in early February, probably began about April. These probable dates fit in with the observations on moulting and non-moulting birds.

The exact duration of moult in individual birds was not calculated but observations on captured birds, and subsequent resightings (of five males and three females), gave a time span of about six to eight weeks. The timing of the appearance of males in new adult plumage before the adult males had completed their moult also gave corroborating evidence.

Development of the frontal spot

The frontal spot in males and females developed at different rates, and was the last adult feature to appear. This has also been noted in the Pied tit (Wilkinson and Wilkinson, 1952).

When the juveniles fledged, the spot was not visible in either sex, but on examination of captured birds a small spot, heavily overlaid by black-tipped feathers in the males and brown-tipped feathers in the females, was discernible. The spot remained at this stage of development in the females throughout the juvenile phase. In the males, however, it became more evident as the bird approached the juvenile moult, and it developed fully during the moult, becoming full-sized and vivid white.

In females, the spot did not develop during the juvenile moult but remained insignificant, still being covered by brown-tipped feathers. This was the only way to distinguish between females in newly acquired adult plumage, and older females. The spot appeared to develop fully over the following months, to a white crescent shape as in the males. (The colouring is contrary to that given by Fleming (1950) and Oliver (1955), who stated that the spot was a pale olive-buff. Of the

13 females in adult plumage handled during this study, all had white frontal spots).

The poor development of the frontal spot during the juvenile stage suggests that it may be disadvantageous to possess a more fully developed spot during this period. The signalling properties of the spot may be important and may assist the juvenile birds, particularly the dependent fledglings, in recognizing the adult birds (see also Chapter 4, Section B). Immelmann (1960) established that a male Red-capped robin, breeding in immature plumage (and hence lacking a red-cap), recognized a red-capped dummy as a possible intruder and attacked it. A dummy lacking the red-cap was not attacked. A similar reaction might be obtained in the Yellow-breasted tit if the juveniles possessed fully developed spots.

7.3.3 Sunbathing

During this study only one observation was made on a tit sunbathing. A male in juvenile plumage on 18-3-78 was observed on a branch of a lemonwood tree 3 m above the ground. He was perched on the branch with his tail spread, wings stretched out horizontally with the flight feathers fanned, and the body plumage fluffed. The branch, on which he maintained this pose for at least 30 seconds, was fully exposed to the sun. Sunbathing has also been observed in the South Island robin at Kaikoura. There was a peak of sunbathing in December, just before the moult, but it was observed as early as August in females (R. Powlesland, pers. comm.).

Potter and Hauser (1974) discussed the main theories as to the function of sunbathing. They believed it was associated with the moult, particularly of the head and upper body feathers, as they observed a number of birds sunbathing while moulting. This does not explain, however, why the wings and tail are fanned.

7.4 CONCLUSION

Moult periods for the Yellow-breasted tit are similar to those for other passerines, although considerable variation is shown (Table 7.3). Juvenile birds having only a partial moult require a shorter time to complete their moult than birds going through a full moult.

Table 7.3. Moult periods for other species of passerines (time in weeks).

Species	Juvenile	Adult	Reference
Yellow-breasted tit	6-8	<12	This study.
Silvereye	<12	12	Swanson, 1971.
Bullfinch *Pyrrhula pyrrhula*	7-9	10-12	Newton, 1966.
Greenfinch	-	12	Newton, 1968.
Chaffinch	-	6	Newton, 1968.
Lesser Redpoll *Carduelis flammea cabaret*	<8	8	Evans, 1966.

\- indicates not given.

One tit was captured on 11-4-78, which had a primary flight feather broken off on the shaft. As this feather had been broken after the bird had completed its moult, it would probably be replaced during the next moult.

CHAPTER 8

FEEDING BIOLOGY

8.1 INTRODUCTION

This chapter is concerned with the feeding behaviour of individual birds. Behaviour while feeding nestlings and dependent fledglings is covered in Chapter 6. Aspects considered included the foraging methods, the sites searched and the types of food taken. As a backup to the observations on the types of food taken, the contents of nestling faecal sacs were examined, as not all prey items captured were identifiable while in the bird's beak. Seasonal changes in foraging behaviour were also monitored.

Five vegetation levels were recognized. These were the canopy, sub-canopy, middle storey, lower understory and ground-storey which included the litter layer. Further details on the composition of these layers can be found in Atkinson (1966) and Gravatt (1971).

8.2 FORAGING BEHAVIOUR

Tits either foraged alone or in pairs and were never seen moving about in the company of other species, i.e. they were solitary feeders. No flocking behaviour was observed during the winter. Only on one occasion was a pair of tits seen in the midst of birds of another species. This happened when a flock of Brown Creepers moved rapidly through the vegetation searching for food, and surrounded the tits for about five minutes before moving on. The tits appeared to take no notice of them and continued feeding.

8.2.1 Foraging height

Prey was searched for at all levels of the vegetation profile, from the litter layer to the canopy. Both sexes, however, were most commonly seen searching in the ground-storey and the lower understorey. Sometimes when searching for prey on the litter layer, the birds moved from vantage point to vantage point within 15 cm of the ground.

Birds did not search in the exposed parts of the canopy but foraged in the area directly beneath the continuous leaf cover (the sub-canopy). Often when the male flew up into the canopy it was to sing from an exposed perch (particularly during the late prebreeding and early breeding season), but prey items were also taken opportunistically. In emergent trees, tits moved about at a height similar to that for the lower, continuous canopy.

The vegetation pattern in the 0-4 m layer, where most of the foraging occurred, was highly varied and ranged from a few scattered shrubs up to dense regeneration where the ground was not visible. Tits were usually seen foraging in areas with scattered ground ferns and regenerating shrubs and an exposed litter layer. Densely vegetated areas were not searched for food. In the lower understorey, shrubs, and the branches and trunks of trees predominated, presenting a wide variety of sites to be searched.

Other studies have also found that foraging occurs from the ground-storey to the canopy. Vegetation structure and type, however, may play an important part in influencing foraging height. Dodgshun (1976), for example, found that tits were evenly distributed from the canopy to the lower understorey but were not observed feeding from the ground in *Nothofagus* spp.-dominated forest in Fiordland. The absence of tits foraging in the ground storey has also been observed in podocarp/rimu dominated forest in Fyffe/Palmer Scenic Reserve, Kaikoura (pers. obs.) where the birds remained high in the trees and were more

commonly heard than seen. This forest-type had very little undergrowth. A similar pattern was noted by Skinner (1978) for the Pied tit in the Waitakere Ranges.

The most comprehensive foraging height data comes from Gravatt's (1971) observations on the Pied tit on Little Barrier Island. Again the birds were found at all levels, but 58.1% of observations were of birds on the ground, with 69.6% of birds seen in the ground-storey or lower understorey. Only 1% of observations were of birds in the canopy. A similar pattern was observed by Riney *et al.* (1959) for the Yellow-breasted tit in Southern Fiordland.

8.2.2 Searching behaviour

Tits did not actively search for prey, i.e. they did not rummage in the litter or disturb bark. Instead, all captures were made through the "watch and wait" strategy, in which an area was scanned until a prey item, either stationary or moving, was seen. It was then captured and eaten.

Two forms of searching behaviour were shown by the tits, and both were seen throughout the year. The commonest method was as follows: the bird flew to a vantage point and scanned the area in front of it. It remained still and did not move its head about. The wings and tail were occasionally flicked. If nothing was sighted, the bird did not change its position on the same perch but flew to another vantage point. This was repeated until a prey item was seen.

Because the bird remained motionless while scanning, keeping the head still became important during windy conditions. The bird achieved this by flexing its legs and neck in time with the motion of the perch it was using as a vantage point (as noted by Gibb (1961) for the Pied tit). Both the body and head were held steady in this manner except during very windy conditions.

Areas scanned included twigs, branches, trunks, leaves and the litter layer. Peeling bark, such as that found on fuchsias, was carefully examined as prey items were often concealed in the folds of the bark.

Vantage points at all angles were used, with vertical branches and trunks being used as frequently as horizontal ones. Tree-stumps, fallen branches on the ground, small shrubs and vines were also used. Along the bush edge and into the more open fields any suitable vantage point was utilized - tree stumps, shrubs, rocks, fence posts and the wires between them, dead branches and trees, dead thistle stems, and the long stems of seeding grasses. In the fields, feeding was slow and deliberate.

Some parts of a territory were searched more frequently than others. This was evident at all times of the year. During the breeding season, a favoured place was the bed of the main stream which passed through several territories. It contained tangles of logs and branches which were searched for two to three hours at a time, in some cases. The bush along the stream-banks was also searched regularly. On one occasion a male disappeared up amongst the roots of a tree left exposed by a slip in the stream-bank and reappeared after 15 seconds. In territories with dense undergrowth covering much of the ground, pairs were often found in the more open areas, scanning the litter layer.

Over the winter period, pairs confined their activities to certain parts of their territory. With the fuchsias losing their leaves during autumn and not regaining them fully until the middle of November, birds moved about in the parts of their territory where permanent leaf-cover was present. In addition, birds with territories on the bush edge were commonly seen feeding in the fields during July and August. The distance moved into the fields probably depended on a balance between the cover, and number of vantage points available.

Search periods from one vantage point ranged from five seconds up to 70 seconds, with five to ten seconds being usual. When changing position the bird always flew to a new perch, often within 30 cm of the last, and, if feeding from the wires of a fence, could move along the fence for 20 or 30 m in this manner.

When searching for items on the ground, the bird flew to the ground only when prey was sighted, landed momentarily, picked up the item and flew back to another perch. It rarely returned to the same perch. If a bird stayed on the ground it remained motionless, sometimes for up to 20 seconds. This was rarely observed.

The second method of searching for prey was a variation of the first, in which the bird moved quickly through the vegetation, pausing and scanning at each vantage point for no more than two to three seconds. This resulted in rapid movement, and probably only prey items which moved were seen and captured. Such behaviour was seen in well-leafed areas and was commonly used by females during the incubation phase of the breeding cycle. After being fed by the male, and before returning to the nest, the female moved rapidly through the vegetation, usually 2-3 m above the ground, for several minutes. This technique was used only in areas with leafy shrubs. The litter was not searched in this way.

When a pair moved about together foraging, they often counter-called. These calls ranged from tick calls, which were very quiet and audible only within a few metres, up to medium call notes (see Chapter 9). When foraging alone, both birds gave medium calls and subsong. The male was particularly vocal at times, giving a wide range of calls, including call notes, subsong and full song. Sometimes both birds remained silent. Bisset (1978) recorded a soft whistle of growing intensity and momentum, given by the female Pied tit, immediately before a prey item was captured. This was not recorded for the female Yellow-

breasted tit during this study.

8.2.3 Prey capture

Various methods were employed to capture the prey once it had been seen. The usual way was to fly over to the item, land briefly, pick it up and either eat it there or fly back to a perch and consume it. If it was taken back to the perch it was usually too bulky or was struggling too much to swallow immediately. Several whacks against a branch solved both problems. Caterpillars were often treated in this manner, probably to break up the body wall. Still-fluttering moths were sometimes fed to fledglings, but larger prey items were nearly always incapacitated before being consumed. Heinekamp (1970) recorded a variation in feeding behaviour - the food was dunked in a stream before being fed to fledglings.

Earthworms presented a different problem as they were too large to eat whole or fly off with directly. Only males were seen capturing earthworms. On seeing a worm, the bird flew to the ground, picked it up and shifted to a branch lying on the ground and proceeded to break the worm up into several smaller lengths.

In one example, a male pounded a 12 cm worm on a branch for three minutes until he broke off a small length. He flew off with this piece of the worm, possibly to feed to the female. Two minutes later he reappeared and continued pounding the rest of the worm against a branch on the ground. He then shifted to another branch and continued to break the worm up. He ate one piece and then flew off with another piece after two minutes. On reappearing 90 seconds later, he broke the remaining length of worm into three pieces and ate them. He then flew off and wiped his beak vigorously on a branch, but returned a few minutes later and continued scanning the area where he had captured the worm. On finding no remaining pieces, he flew off. Throughout the whole episode

the male moved about only on branches forming part of the litter layer. In some cases these raised him no more than 5-10 cm off the ground. Other prey can also be dealt with on the ground. M'Lean (1911) recorded a male Pied tit struggling on the ground with a large moth which had a wing span of 3.5 inches (8.9 cm). Therefore the size of the prey does not deter a tit from attacking it.

Three other forms of prey capture were seen, all much rarer than the usual method. These were:

1) Hovering.

Hovering occurred when a tit saw prey on a branch or leaf. Rather than landing on the substrate to capture it, the bird flew over to it directly, hovered briefly as it captured the item and then flew back to a perch and swallowed the item. This was also observed by Riney *et al.* (1959).

2) The fly-past

Sometimes a tit picked prey off a leaf or fern frond as it flew past. No hovering was involved. This action was termed the fly-past.

3) Hawking

The rarest form of prey capture was hawking. This occurred when the bird saw an insect flying past, and reacted by flying out and up to it, capturing it in its beak and returning to a perch. Dependent fledglings were particularly inept at this mode of prey capture. Adult tits were more successful than fledglings, but not every hawking foray was successful. Tits do not appear to be adapted for exploiting food sources in this way. M'Lean (1911), however, observed the Pied tit taking slow-flying insects on the wing, and remarked that they showed much dexterity in doing so.

Prey were seen and captured from distances of up to about 10 m. This was particularly evident when birds flew out from the bush edge into the fields to capture prey. Usually, within the bush shorter distances were travelled and, when searching the litter layer, prey were captured from distances varying between 10 cm and 5-6 m. Potts (1883) and Soper (1976) recorded tits moving 12-15 m to capture prey. The South Island fantail hawks insects 2-15 m from the perch (Ude Shankar, 1977).

Gravatt's (1971) results for the Pied tit showed that they obtained 52.4% of their food from the litter layer. Birds feeding on the wing (hawking and hovering) accounted for 11.3% of the observations, with the balance of 36.3% being of birds feeding from trunks, branches, twigs, leaves and terminal shoots. A similar pattern was seen in the present study, but with fewer items being taken on the wing, and more from the trunks, branches and leaves.

8.2.4 Foot trembling

Foot trembling was observed in tits in juvenile and adult plumage, and of both sexes. It occurred when a bird was perched on a horizontal branch, and involved the raising of either foot slightly above the surface and trembling it for about two seconds. This was not seen while a bird was on the ground. Wing drooping (see also Chapter 4, section 4.15.2) was also seen at the same time, but the two events may not have been connected. Foot trembling was seen throughout the year but most commonly during the breeding and post-breeding seasons.

It has also been observed in the South Island robin (Edgar, 1961; Soper, 1976; R. Powlesland, pers. comm.), being described by Soper as "placing one foot on the ground slightly forward of the other, quivering it rapidly for a second or two, pausing, then repeating the action". Best (1975) mentioned it occurring in the Snares Black tit

while the bird was standing on the litter layer, and Stewart (1977) has also observed it in the Australian Flame robin.

Therefore, foot trembling appears to be a phenomenon common to several members of the genus. The function of foot trembling, however, is subject to conjecture, although it is commonly associated with food gathering when seen in wading birds (Heather, 1977). The vibrations resulting from the trembling supposedly disturb prey, causing them to move. There is little evidence to support this idea from the observations made on New Zealand tits and robins, but Stewart (1977) stated that when the Flame robin pattered its foot rapidly on the ground, it pounced on any insects disturbed. However, the observations made on the Yellow-breasted tit suggested that the foot did not touch the substrate while it was being trembled. Therefore, there may be several different types of foot trembling (as outlined by Heather, 1977), possibly used in different contexts and quite possibly not associated with food gathering.

8.3 FOOD TYPES

8.3.1 Items observed taken

Yellow-breasted tits fed on invertebrates throughout the year. During the winter, vegetable matter may also have been taken, as birds were sometimes seen pecking repeatedly at pepper tree berries. The proportion of vegetable matter in the diet was not established. Poole (1951) observed tits feeding on the berries of small-leaved coprosmas in Fiordland.

A wide variety of invertebrates were taken, although not all could be identified when they were in the bird's beak. The only items broken-up on the ground were earthworms (Annelida: Oligochaeta). All other items were consumed immediately, or eaten once the bird had

returned to a perch.

Prey types taken included: spiders (Arachnida: Araneida), beetles (Coleoptera: not identified while in the beak), caterpillars and moths (Lepidoptera), various Diptera (including Tipulidae, Muscidae, Calliphoridae, Tachinidae, and other unidentified forms) and bees (Hymenoptera: Apoidea).

Caterpillars were a common food, being easily recognizable while in the beak. They were usually whacked against a branch before being eaten. Craneflies were also obvious because of their long legs and wings.

When birds were searching for food for themselves, prey were consumed as they came across them. When feeding nestlings, however, several items were collected by the adults before returning to the nest. Again prey were collected as the birds searched, so that a mixture of items was taken back to the nest. When feeding dependent fledglings, single items were fed.

Yellow-breasted tits have a similar diet throughout their range. In addition to the above items, the larvae of beetles and grasshoppers (Potts, 1882, 1883; Smith, 1893) and millipedes (Oliver, 1955) were also taken. Buller (1888) found the stomachs of tits full of small diptera, coleoptera, caterpillars and aphids.

8.3.2 Faecal sac analysis

Eighty nestling faecal sacs were collected from two sites:

1) 70 from the rims of three nests, or the ground below the nests, during the days after the chicks had fledged; and
2) 10 from where the adult birds had dropped them after removing them from the nest.

These were teased apart and any identifiable material removed. Figures 8.1B and C show examples of some of the prey remains

Figure 8.1

A. Two species of beetles preyed upon.

B. Prey remains identified from faecal sacs.

FIGURE 8.1

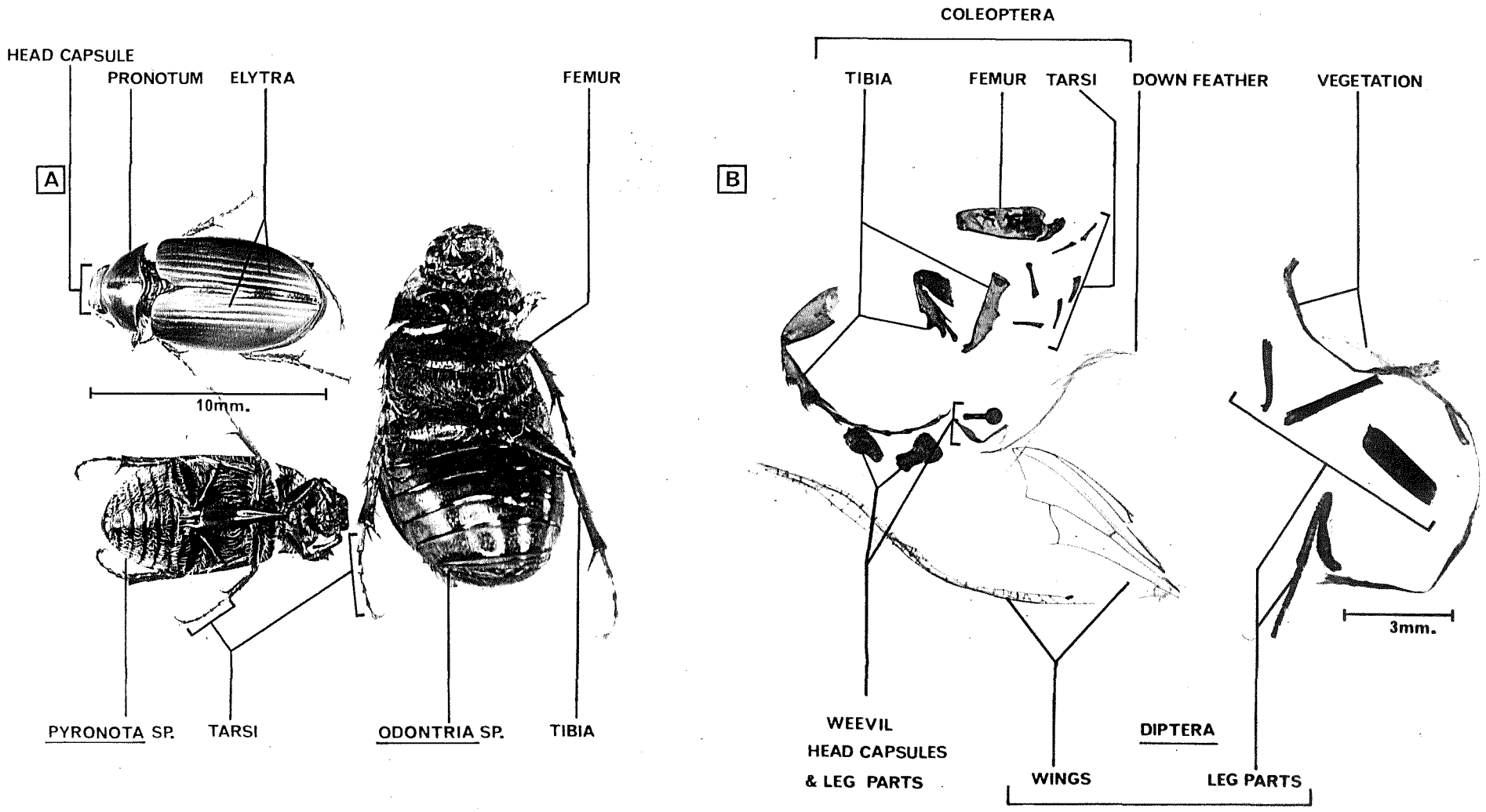
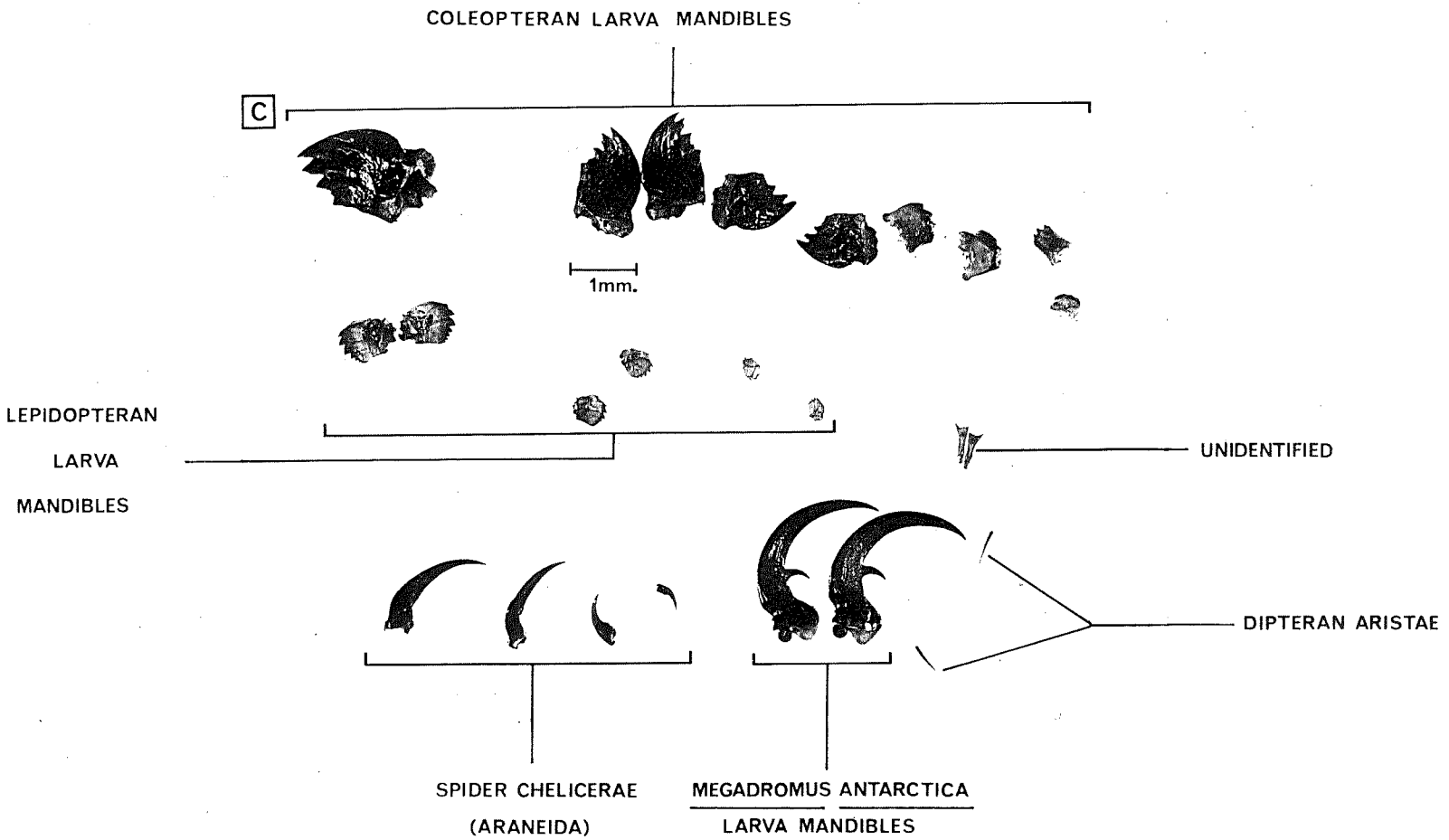

HEAD CAPSULE
PRONOTUM
ELYTRA
FEMUR
A
10mm.
PYRONOTA SP.
TARSI
ODONTRIA SP.
TIBIA
COLEOPTERA
TIBIA
FEMUR
TARSI
DOWN FEATHER
VEGETATION
B
3mm.
WEEVIL
HEAD CAPSULES
& LEG PARTS
WINGS
DIPTERA
LEG PARTS

Figure 8.1 (continued)

C. Prey remains identified from faecal sacs.

FIGURE 8.1(cont.)



found in the faecal sacs. Generally, only those parts of a prey item's body which were heavily sclerotized remained recognizable. Other parts were too broken-up, although dipteran wings sometimes remained nearly intact.

From the remains identified it was established that two cockchafers (Scarabaeidae) were commonly taken. Remains of these beetles were the commonest items in the faecal sacs, and were identified as the Green Manuka beetle (*Pyronota* sp.) and a large brown beetle (*Odontria* sp.) (Figure 8.1A). Parts of these beetles identified included the head capsule, pronotum (often retaining its green colour in the manuka beetle), elytra, abdominal sterna, tarsus, tibia and femur. The mandibles of the adult beetles were not recovered, but the mandibles of larval forms of other species were. The range of sizes is shown in Figure 8.1C. One pair of mandibles from the probable last instar of *Megadromus antarctica* was also found. This animal would have been about 34 mm in size (P.M. Johns, pers. comm.). Other coleopteran remains were those of at least three species of weevils (Curculionoidea), the commonest parts being head capsules and elytra, with leg parts appearing less frequently.

The other common mandibles found were those of caterpillars (Figure 8.1B). These varied in size, illustrating the size range of caterpillars taken.

Dipteran remains were also very common, with the most plentiful parts being sections of legs. The long legs of tipulids were immediately recognizable. In addition, head capsules, bristles, probable aristae (Borror and De Long, 1971) and tipulid eggs were also found. Parts of wings appeared irregularly.

The only identifiable parts of spiders were the chelicerae.

Non-animal remains also appeared. These included lengths of vegetation which were probably ingested when the chicks were fed, and

probable natal down feathers (Lucas and Stettenheim, 1972). These were sometimes seen attached to the contour feathers in newly fledged chicks.

Therefore, the remains of a wide range of prey types appeared in the faecal sacs, with coleopteran, lepidopteran and dipteran remains present in nearly every sac.

8.4 SUMMARY AND DISCUSSION

An ideal predator, in order to maximize fitness in the long term, ought in the short term to maximize net rate of energy (or food) intake while foraging (Krebs and Cowie, 1976).

The observations made on the niche exploitation pattern of the Yellow-breasted tit suggested that it conformed to the above theory. Tits displayed behaviour shown by food generalists. Birds in Type A territories are often food generalists (Morse, 1971), as they have to obtain the majority of their food within their territorial boundaries. Tits hunted at random, rather than by expectation, shifting to a new vantage point away from the area just scanned. No evidence was seen to suggest that birds travelled shorter distances to new perches if prey was sighted from the previous perch than if prey was not sighted, as seen in the Eastern Bluebird *Sialia sialis* (Pinkowski, 1977). Prey were taken as the birds came across them, resulting in items being taken in the proportions in which they occurred, i.e. they displayed fine-grained behaviour (MacArthur and Pianka, 1966). Some parts of the territory were searched more regularly than others, however.

Although only one basic searching pattern was used (i.e. "watch and wait") it was very successful, and when it was combined with the four different ways of catching the prey, a wide variety of invertebrate habitats was open to exploitation. The range of prey items taken, both in size and species, was established from observation and faecal sac

analysis. In addition, other unidentified prey items were taken.

The feeding behaviour of the Yellow-breasted tit differed from that of the Snares Black tit. Best (1975) recorded the Black tit hopping about on the litter and peat layer in open *Olearia* forest. Such behaviour was not observed during the present study. In addition, only 25% of the observations made by Best were of birds feeding from the ground, with the majority of observations being of birds feeding from trunks and branches. The leaves of the canopy were rarely approached. Observations on birds in forest with a denser ground understorey were not recorded.

Tits throughout the New Zealand region show a wide variability in their feeding heights (see also 8.2.1). This may be influenced by the vegetation type, and its profile and height.

CHAPTER 9

VOCALIZATIONS

9.1 INTRODUCTION

Yellow-breasted tits produce a number of vocalizations, the most distinctive of which is the male's song. This is the main vocalization commonly referred to in the literature (Andersen, 1926; Fleming, 1950; Riney *et al.*, 1959; Soper, 1976), with occasional references being made to other less easily defined calls (Fleming, 1950; Poole, 1951).

Until the present study, no investigation into the variety and structure of calls given by Yellow-breasted tits had been carried out. Bisset (1978) recorded and analyzed song, subsong, and 11 types of calls given by the Pied tit, and determined the context of some by carrying out playback experiments. In addition, she examined the consistency and uniqueness of a male's song and the variability between songs of neighbouring males. She also considered the geographic variation between songs of non-neighbouring populations. Hay (1975) briefly catalogued some vocalizations of the Chatham Island tit, recognizing seven types: simple, aggressive, submissive, begging, downscale, calls given while boundary patrolling, and song and subsong.

In this chapter the vocalizations given by the Yellow-breasted tit, from the nestling stage onwards, are catalogued. Sonagraphic analysis was also carried out so that the relationships between different calls could be established. The vocalizations are covered under two sections. The first examines the variety of calls, and the circumstances in which they were given. The second discusses song and subsong, and examines the development of juvenile song into adult song. The

similarities and differences between songs of neighbouring males are also investigated. Comparisons are also made with the vocalizations given by the Pied tit.

9.2 METHODS

Representative examples of the calls made by different tits were recorded throughout the present study. The conditions under which they were given and the reaction of other tits to them were also noted.

All recordings were made with a Philips EL3302 portable cassette taperecorder, using an EL3797/50 microphone with a range of 80-10,000 Hz ± 6dB. More elaborate equipment was not used because a detailed study of the structure of the calls was not within the scope of this thesis. Where possible, recordings were made as close to the bird as practicable (often within 2-3 m). Further details on techniques and equipment used to record bird vocalizations are outlined in Gulledge (1976).

Selected vocalizations were analyzed on a Kay Electric Company Sonagraph (Model 6061-B), using the narrow band-pass filter setting to enhance frequency resolution, at normal speed. This allowed 3.1 seconds of sound to be reproduced in the 80-8000 Hz range. In addition, some calls were analyzed in the 160-16,000 Hz range, allowing 1.5 seconds of sound to be reproduced. This gave a clearer picture of the structure of a call as it was stretched along the time axis. The principles and mechanisms involved in the production of sonagrams are discussed in Davis (1964) and Greenewalt (1968).

Because the vocalizations analyzed were not recorded under ideal conditions, or on ideal equipment, some sonagrams show varying degrees of background noise, resulting primarily from wind, running water and cicadas.

9.2.1 Some definitions

The vocalizations of Yellow-breasted tits were constructed of the following:

Notes: single marks on the sonagram.

Syllables: these are composed of at least one note. A number of syllables form a song phrase.

Phrases: complete units of sound, as in song phrases.

9.3 CALLS

Three groups of calls were distinguished on the basis of their structure and the contexts in which they were used. These were call notes, nestling and dependent fledgling calls, and complex sounds.

9.3.1 Call notes

Call notes are mono- or disyllabic and practically never consist of more than four or five notes. When uttered in longer series, there is no clear organization of the sequence into bursts of definite lengths (Thorpe, 1961).

Five types of call notes are described in this section. In addition, distinctive forms of some call note types were recognizable, but their classification was arbitrary because their contexts remained obscure.

In the field these calls were distinguished by the emphasis placed on them, their intensity, and the pattern in which they were emitted. All the calls analyzed in this section fell between 6 and 9 kHz and had a similar structure.

a) Tick calls

Tick calls were the quietest and briefest calls given by tits,

being audible only within 3 or 4 metres of the bird. They were given alternately by a pair of birds as they moved about within a few metres of each other, searching for food. This resulted in counterticking.

Ticking was heard throughout the year but most commonly in the two weeks before the start of, and during, the breeding season. Juvenile pairs were also heard counterticking when they first occupied a territory during the late breeding, and post-breeding seasons.

The male was sometimes heard ticking by himself during the breeding season but always within a few metres of the nest.

Tick calls appeared to function as a contact call between the members of a pair.

b) Simple calls

Pairs of tits and individual birds emitted simple calls as they moved about. They were given at irregular intervals, usually singly, but sometimes in groups of two or three. Some calls were so quiet that they could be heard only within 3-4 m of the bird, whereas others were audible up to 30 m away from the bird calling.

Simple calls were used in a variety of contexts. They were commonly given at random by individual birds as they moved about searching for food. Members of a pair also countercalled when they were foraging in close proximity to each other, particularly when they could not see one another because of the vegetation. Females building nests also gave them irregularly, even when the male was not in the area.

A male, when coming in to feed the female while she was nest-building or incubating, alerted her to his presence by emitting simple calls. She responded by stopping what she was doing, sometimes calling in reply, and flying over to him to be fed.

Both sexes gave simple calls when flying up to the nest to feed nestlings. The nestlings reacted with begging calls, which began before the parent bird reached the nest when they were close to fledging.

These calls were also given when the adults were feeding dependent fledglings. They served two functions: they informed the adults as to the fledglings' whereabouts as the fledglings responded with begging calls and, at the same time, alerted them that they were about to be fed.

Bisset (1978) suggested that simple calls given by individual Pied tits may have acted in a sequestrative manner. This may also apply in the Yellow-breasted tit. They also acted as contact calls between birds.

Three arbitrary types of simple calls were recognized as intermediate forms were also heard. They were identified on the basis of the intensity with which they were emitted, and the emphasis placed on them.

Quiet calls

These were most commonly given by individual birds and carried for only a few metres (Figure 9.1A).

Medium calls

These were the commonest simple calls emitted by tits, and were heard at all times of the year as birds moved about foraging. They were also given when feeding nestlings and dependent fledglings. Counter-calling between members of a pair nearly always involved calls of this type.

Loud calls

These were occasionally given by individual birds and carried for up to 30 m. Their function was not determined, but they were sometimes used as location calls when an adult was feeding near-independent fledglings.

c) Adult challenge call

The adult challenge call was given by adult males in response to probable disturbance or novel stimuli. It was audible up to about 50 m from the bird calling and was emitted at irregular intervals.

Figure 9.1

Simple calls. Recording dates given in brackets.

A) Quiet call notes (20-12-77)

B) Juvenile challenge call (12-1-79)

C) Low intensity alarm call (6-2-78)

D) High intensity alarm call (18-3-78)

Figure 9.2

Dependent fledgling calls. Recording dates are given in brackets.

A) Hunger call (16-1-79)

B) Chrup and flying-chrup calls (22-1-78)

Figure 9.3

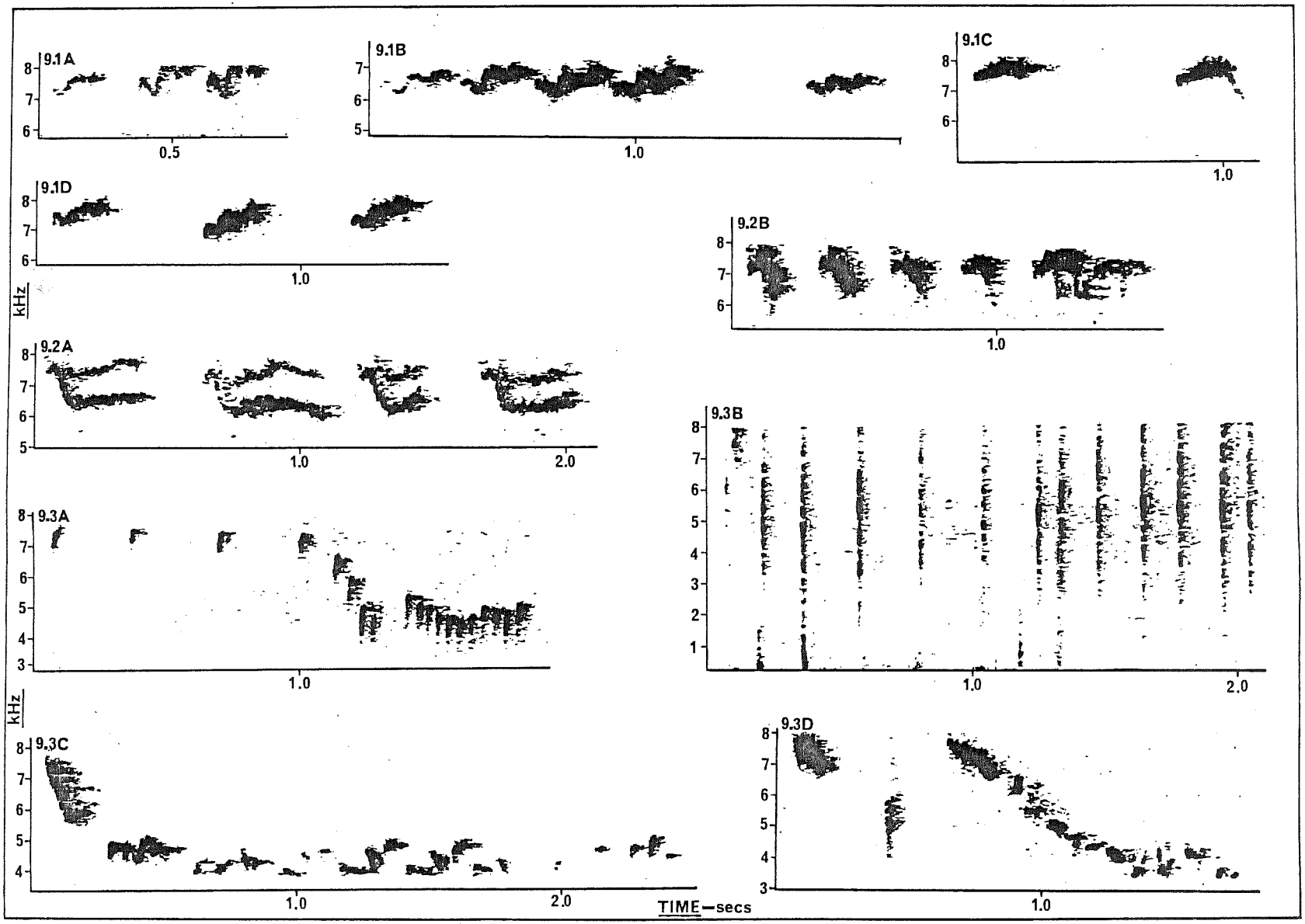
Complex sounds. Recording dates are given in brackets.

A) Staccato chuck (24-9-78)

B) Bill clicks (12-1-79)

C) Feeding twitters (3-11-78)

D) Feeding twitters (8-11-78)


9.1A
9.1B
9.1C
9.1D
9.2A
9.2B
9.3A
9.3B
9.3C
9.3D
kHz
TIME—secs

This call was exchanged between males during border disputes.

d) Juvenile challenge call

This was one of the commonest calls used by independent juveniles and newly moulted immatures, and was the loudest call emitted by tits of any age. Females gave it only while in juvenile plumage.

Challenge calls were given by birds maintaining territories, in response to any disturbance or intruding tit. They were also elicited when a tape of a male song was played near them.

Figure 9.1B shows the structure of the call. Simple loud calls, and adult and juvenile challenge calls all had a similar structure.

e) Alarm calls

Alarm calls of varying intensities were heard throughout the year and consisted of the same note repeated at regular intervals.

They were given in two different situations. Firstly, when adult birds were feeding dependent fledglings they sometimes moved about giving an alarm call at the intensity of a medium call note. This call was often given when I approached the birds too closely. However, the adults continued foraging and the fledglings still begged from them. This may have been a low intensity alarm call given in novel, non-threatening situations (Figure 9.1C).

A more intense call was given in response to more threatening stimuli (Figure 9.1D). These included birds flying over the study area (Australasian Harriers and magpies) and native pigeons crashing through flimsy canopy foliage. The number of consecutive calls given varied from about six upwards. A male, on one occasion, gave 80 closely-spaced calls. Dependent fledglings responded by becoming silent.

9.3.2 Nestling and dependent fledgling calls

The main calls given by tits at this stage of development were begging calls. They were heard from when the nestlings hatched until

one to two weeks after the fledglings had become independent. Adult females also gave begging calls. Several other calls were also given.

a) Nestling calls

On hatching, nestling calls were barely audible, but become louder as the nestlings grew. Immediate begging calls were elicited as soon as the parent flew up to the nest to feed them. In the few days before fledging they gave begging calls as soon as an adult called or sang near the nest site, and continued calling for a few seconds after the parent had left the nest.

These calls were relatively unstructured and were located between 7 and 9 kHz.

b) Dependent fledgling calls

Three distinctive types of calls were given by dependent fledglings.

Hunger or begging calls

The hunger call was used when begging from a parent bird, and was given in association with the typical begging posture. For the first few days after fledging it was given almost continuously, even when the adult birds were not present. After this period it was given increasingly only in response to the calls or song of a parent, or on seeing another tit. The call increased in intensity and frequency when the fledgling was approached by an adult. Hunger calls were also used when chasing after adult birds.

During the first week of independence, hunger calls were often mixed in with juvenile song and subsong, as the birds moved about searching for food.

Figure 9.2A shows the characteristic shape of a hunger call. It has a structure similar to that for the same call for the Chatham Island tit (Hay, 1975).

This call was also used by adult females when begging for food off their mates.

Chrup calls

Chrup calls were not associated with begging for food, but were given by fledglings while they remained on one perch for any length of time. They were much briefer than a hunger call and were emitted individually and at irregular intervals. A chrup call was sometimes given in response to an adult call note.

This call fell within the 6-9 kHz range.

Flying-chrup call

This call was heard only when fledglings flew from one perch to another, but not when chasing adults. It consisted of a series of chrup calls repeated at very short intervals and was commonly heard during the first 10 days after fledging.

Figure 9.2B shows the structure of this call.

9.3.3 Complex sounds

This section includes a number of different sounds, all of which had a more complex structure than those in the previous two sections.

a) Distress call

Distress calls were emitted by some birds as they were removed from mist nets. The call consisted of a harsh squeal similar to that described and illustrated by Bisset (1978) for the Pied tit, and covered a wide frequency range.

b) Aggressive sounds

Two forms of aggressive sounds were heard. The first type, the staccato chuck, was commonly used during chases within a territory, during border disputes and, more rarely, by individual birds as they moved about feeding. During intensely aggressive interactions, usually involving physical contact, the second type of sound, bill clicks, was

given.

Staccato chuck

Staccato chucks were given by both sexes, from the dependent fledgling stage onwards. They were composed of rapidly repeated notes of short duration, often given in a descending fashion (Figure 9.3A). The staccato chuck is equivalent to the Churr call of the Pied tit (Bisset, 1978).

Bill clicks

During extremely aggressive encounters, for example when two birds were locked together on the ground with their claws entangled, bill clicks consisting of a repeated snapping together of the mandibles were given. Staccato chucks were often heard before, and sometimes after, the encounter.

Figure 9.3B shows the sonagram resulting from bill clicks. Note the wide frequency range and short duration of each click.

Individual bill clicks were heard when a bird was searching for prey and missed the item it attempted to capture.

c) Feeding twitters

During the breeding season when the male approached the female to feed her, he gave a few call notes or some song phrases. When he fed her he sometimes let out a brief twitter as he placed the food into her open beak. This was audible from only a few metres away and was often drowned out by her begging calls.

Two examples of feeding twitters are shown in Figures 9.3C and D. Note the descending nature of the call and its variable structure. It also varied in length.

9.3.4 Comments

Two further calls were heard given by females. However, because they were heard only once, good descriptions were not obtained.

One was used when a female chased a Grey Warbler away from her nest, and may have been an aggressive type of call. The other was heard when the female of a pair called to the male as they were foraging. It may have been a form of feeding twitter.

Calls emitted by juveniles and newly moulted immatures in the first part of the post-breeding season were usually louder than those given by adult birds. Simple calls, similar to those given by adult birds, were first heard in near-independent fledglings.

9.4 SONG AND SUBSONG

Song is a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time (Thorpe, 1961). In the Yellow-breasted tit this was heard as a musical warble.

Subsong, however, has a more diffuse meaning, with a wide variety of definitions being used (Armstrong, 1973), but includes song types other than full song. Two broad types can be recognized.

Developmental subsong

This is the song given by juvenile tits of both sexes before they moult into adult plumage. After the moult, full song develops. Juvenile song varied in intensity and was most commonly given by birds maintaining territories. It did not sound like full song.

Nondevelopmental subsong (or Foraging chatter)

Nondevelopmental subsong covered a particular group of calls characteristically heard in immature and adult birds as they moved about feeding. Dependent fledglings and juveniles also gave a form of it. These calls were not given in a territorial context, were usually quiet and did not develop into adult song.

Features common to both types of subsong were that they were usually quieter and covered a wider range of frequencies than full song. They consisted of an assemblage of non-stereotyped calls of variable length. Full song, as given by adult males, fell within a narrow range of frequencies, was stereotyped and often loud. Developmental subsong sounded like a weak warble whereas nondevelopmental subsong sounded like quiet chatter.

In dependent fledglings, which began singing a few days before independence, both forms of subsong were sung together at random. However, after independence, a gradual separation of the two forms took place, so that shortly after the juvenile moult had been completed they had crystallized into two distinctive vocalizations (full song and non-developmental subsong), sung independently of each other.

Full song usually started spontaneously, but on rare occasions foraging chatter was given beforehand. The presong chatter of the Pied tit appears to be similar to the foraging chatter of the Yellow-breasted tit. Bisset (1978), however, associated it with a slow increase in motivation towards singing. This was definitely not the case for the Yellow-breasted tit.

Once attained, full song remained the same throughout the year, showing no change in pattern after the completion of breeding activities. This can be contrasted with some other bird species in which the song of the males passes through a developmental stage before every breeding season, e.g. White-crowned Sparrows *Zonotrichia leucophrys nuttalli* (Baptista, 1975) and Fox Sparrows, *Passerella iliaca* (Martin, 1977).

9.4.1 Nondevelopment subsong (Feeding chatter)

Nondevelopmental subsong consisted of a mixture of different calls repeated in phrases of varying lengths. In immature and adult birds, two distinctive patterns were evident and could be recognized immediately.

Sonagraphic analysis showed that they were made up of a limited number of complex sounds very different from those described in section 9.3. The two forms were termed the burble and the chuckle, each associated with notes having a characteristic structure.

a) The burble

This was the most frequently heard of the two call-types and consisted of two types of notes. The first had a double-structured form (Figure 9.4A), lying between 4 and 7 kHz. This note was repeated up to about six times in a row. A very distinctive note, composed of up to three parts, followed the first type of call (Figure 9.4B). It fell within the 4 to 9 kHz range. A repeated series of these two note-types resulted in the burbling sound.

b) The chuckle

This call was also made up of two distinctive note-types. These are shown on Figure 9.4C. The first note-type (marked a) varied in structure, but consisted of up to three parts, and fell between 5.5 and 10 kHz. Several of these were repeated until the second note-type was given (marked b). This call was a form of staccato call, made up of very closely spaced notes lying between 5 and 8 kHz. It was never repeated in sequence, but was always placed in amongst call-type a.

Nondevelopmental subsong was sung throughout the year by both sexes. In addition to the burbles and chuckles, call notes, staccato chucks and occasional song phrases were included at random in the repertoire. Adult males often sang in this way for 10-15 minutes at a time as they searched for food.

Figure 9.4

Nondevelopmental subsong (Feeding chatter). Recording dates are in brackets.

A) The burble (25-10-78):

The 1st call-type is labelled a. Note the harmonics between 9 and 12.5 kHz.

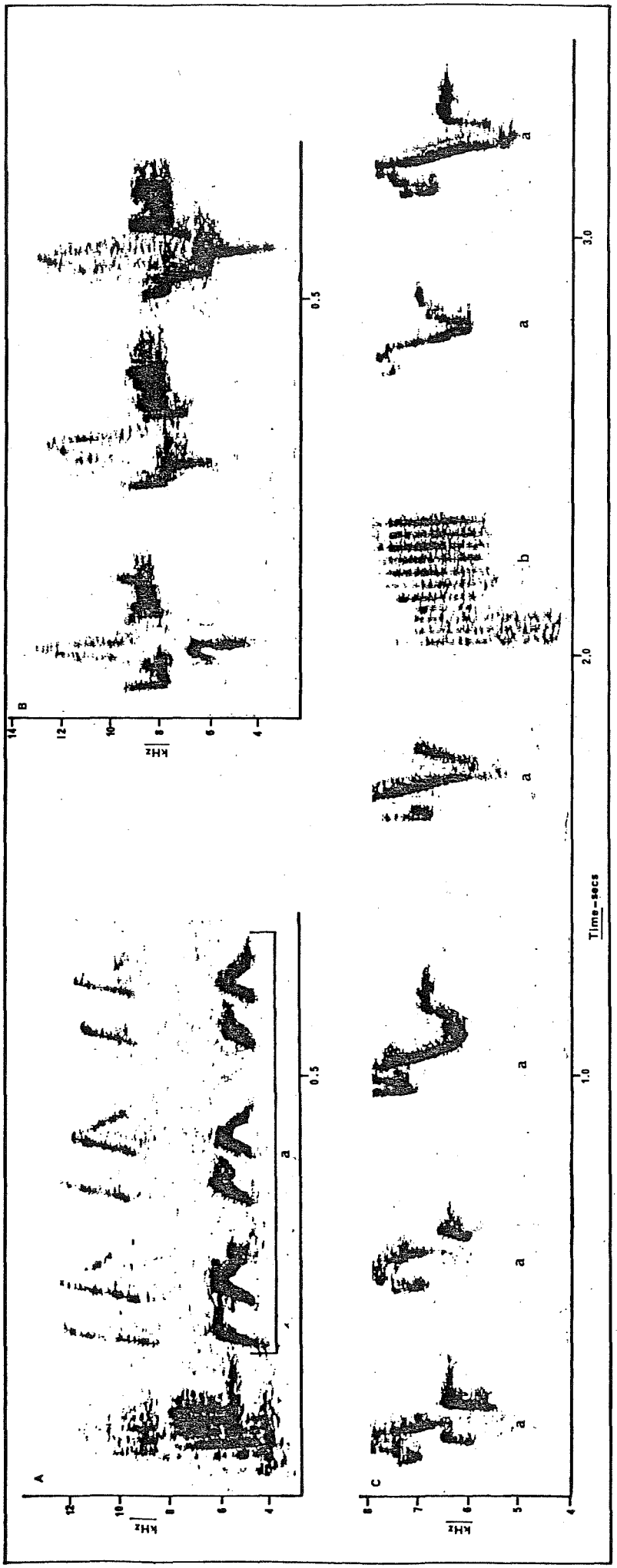
B) The burble (25-10-78):

The 2nd component of the burble.

C) The chuckle (28-12-77):

a) note-type a.

b) note-type b.


A
B
C
kHz
Time-secs
a
b
0.5
1.0
2.0
3.0

9.4.2 The development of song (Developmental subsong)

Dependent fledglings and juveniles of both sexes sang regularly and, although the songs sounded like a weak warble, differences between male and female song were discernible.

a) Female subsong

Females sang regularly before the moult, particularly if they were maintaining a territory. However, with the onset of the moult the singing rate decreased rapidly until the vocal repertoire consisted mainly of simple calls.

The song phrases were of irregular length and had no particular pattern, with some notes covering a wide frequency range (up to 4 kHz). All the notes fell between 2.5 and 7.5 kHz (Figure 9.5A, B, C).

Females sang for several minutes at a time and often interspersed the phrases with call notes and staccato chucks.

b) Male subsong

Song given by dependent males was difficult to separate from nondevelopmental subsong. It covered a wide range of frequencies (2-9 kHz), and was relatively unstructured with notes repeated at random. It bore no resemblance to adult male song.

Figure 9.6A, B, C shows the structure. Elements of both types of subsong can be distinguished.

Independent males

After independence, and as the moult approached, the song changed markedly. The phrases became more structured, with notes falling within a narrow frequency range (2.5 - 5.5 kHz), but still being repeated at random (Figure 9.7A, B).

Figure 9.5

Independent juvenile female subsong (female 141, recorded 6-3-78).

A) Staccato chuck

B) Song phrase

C) Song phrase

Figure 9.6

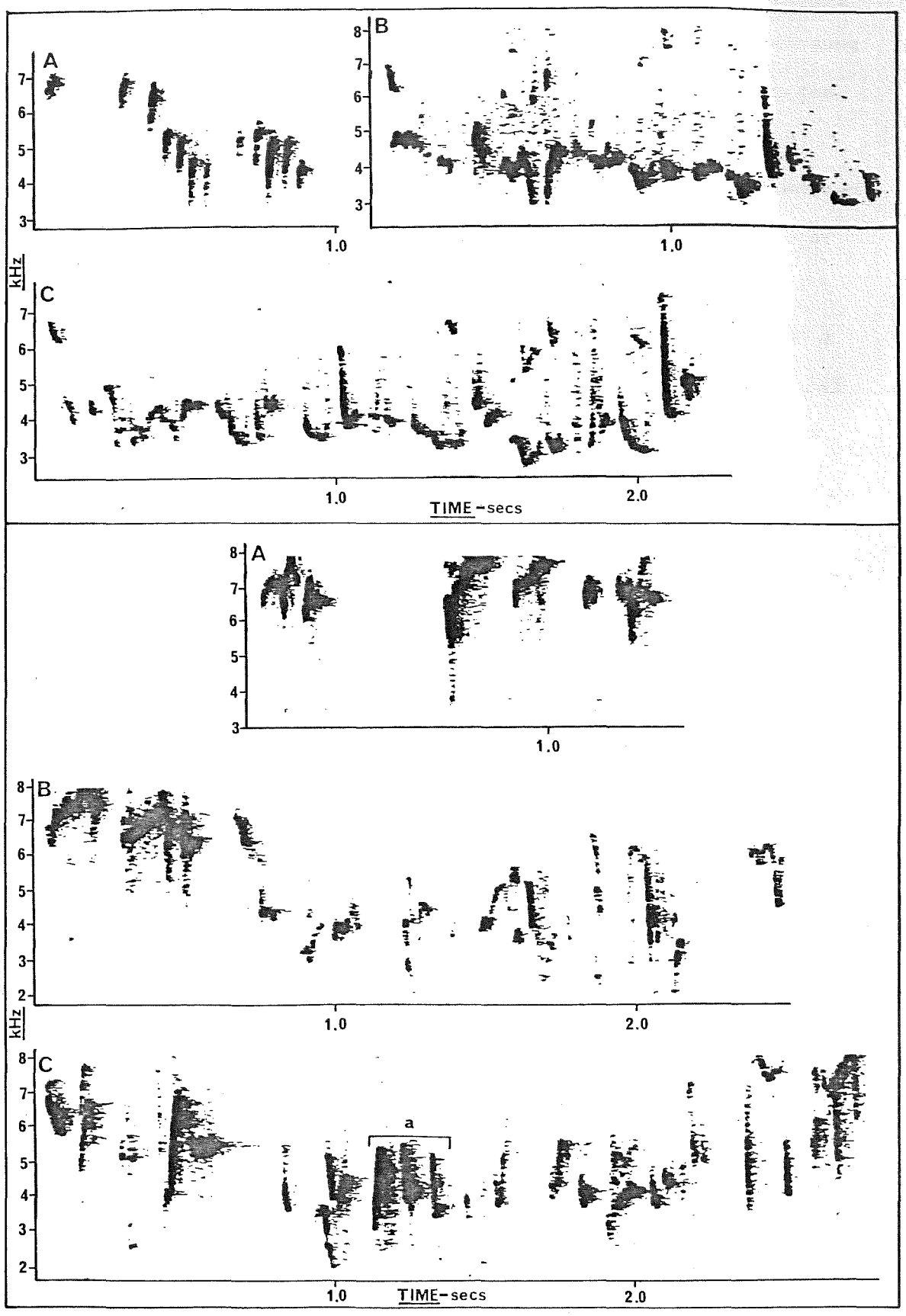
Dependent juvenile male subsong (male unbanded, recorded 16-1-79).

A) Random calls

B) Song phrase

C) Song phrase

a) elements of nondevelopmental subsong.


A
B
C
kHz
1.0
2.0
TIME-secs
a

9.4.3 The transformation from juvenile male to adult male song

During the juvenile moult the song remained similar to that sung before the moult. Birds often sang loudly as they moved about in the trees.

Shortly after the moult had been completed, the song had evolved into a form resembling that sung by adult males. The phrases were of regular length but the structure still showed some plasticity.

Male 126, for example, banded while in juvenile plumage, had a repertoire of four or five different song phrases after the moult, all of which were sung at random. This period of plasticity appeared to last for only a few weeks. Later, in the following breeding season, this male had only one song type, i.e. all the phrases had the same structure. This phrase, however, was also the one sung most frequently after the juvenile moult. Figures 9.8A, B and C show three of the phrase-types sung by this male. The primary difference was in the central part of the phrase where variability was shown in note structure and placement. Figure 9.8C is the song-type later sung exclusively by this male. All the notes, apart from the one at the start of the phrase, fell between 3 and 5.5 kHz.

9.4.4 Adult song

a) Female song

On attaining adult plumage females sang infrequently, and when they did sing, their song sounded like a very much quieter version of the male song. The female sometimes sang during the breeding season, particularly when returning to the nest to incubate or feed nestlings.

b) Male song

Males sang spontaneously from August until early January, and sang throughout their territories and along their shared boundaries. During December and January a quiet version of full song was often sung.

Figure 9.7

Independent juvenile male subsong (unbanded male, recorded 28-1-78).

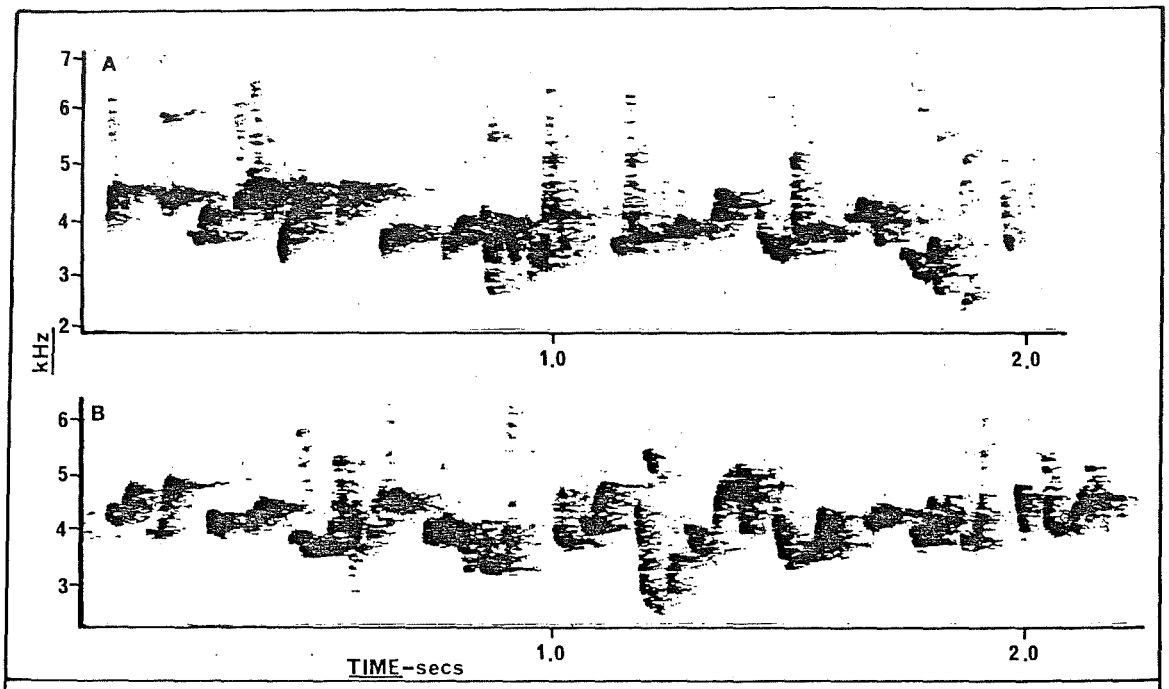
A) Song phrase

B) Song phrase

Figure 9.8

Immature male song (male 126, recorded 21-3-78).

The dominant phrase-type is shown in C. The major differences in the other two phrases are indicated.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kHz
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2
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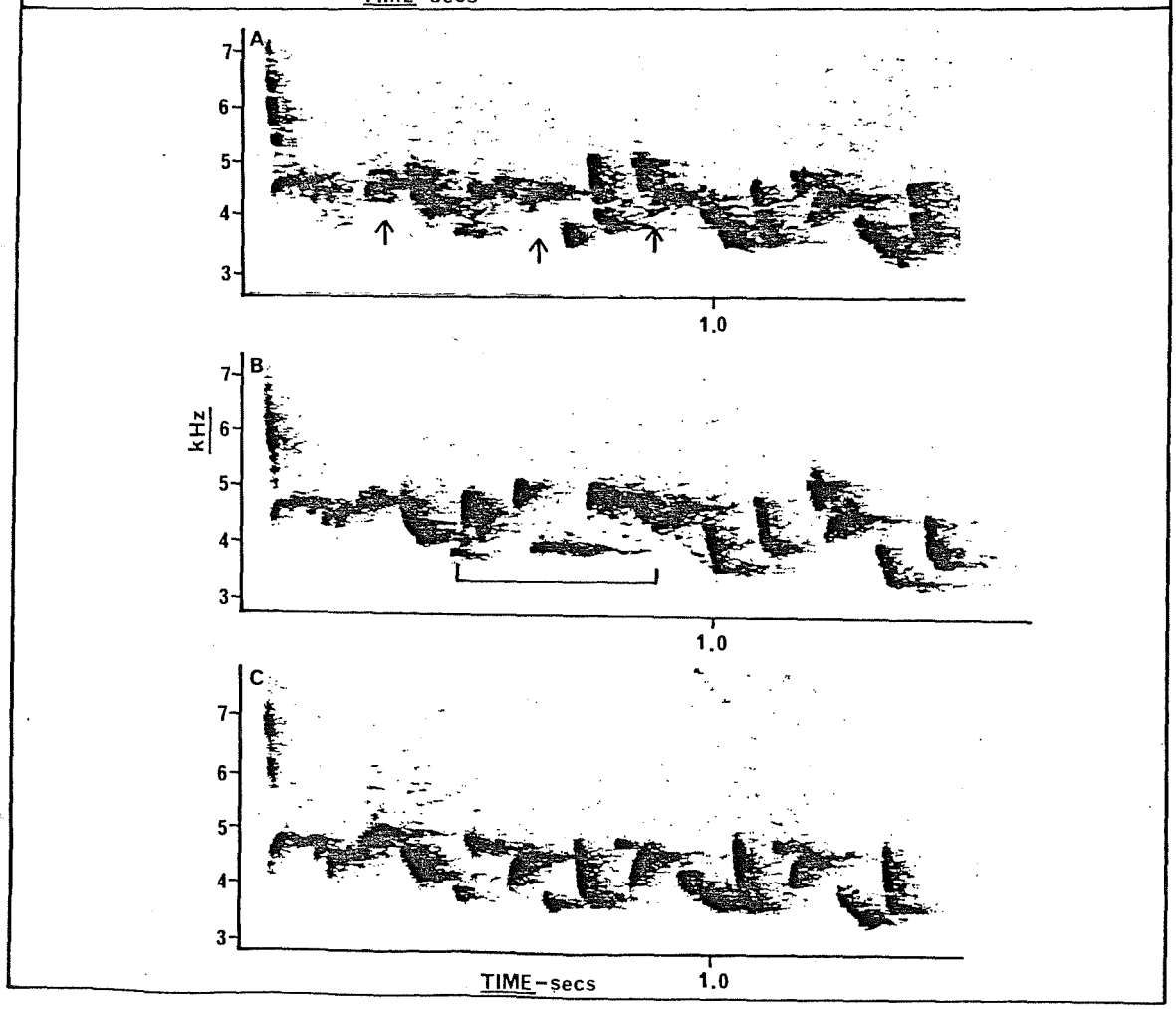
TIME-secs


A
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kHz
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3
1.0
TIME-secs

After breeding activities had ended they became quiet, and displayed no reaction towards a tape of a song played in their territories. Immature males sang irregularly while the adults were moulting. There was a brief resurgence of singing in April after all birds had completed their moult.

During the winter months, spontaneous song was heard intermittently. Some males sang in reply to a taped song, whereas others ignored it.

The Song

The song of each male within the study area was stereotyped, with each song phrase being made up of a number of notes or syllables. These phrases were repeated at regular intervals.

Thirteen of the 15 males recorded each had one song-type, i.e. the phrases all had the same structure. Two of the males had two song-types which they sang at random, although one was repeated more regularly than the other. The two phrase-types sung by male 118 are shown in Figures 9.9A and B. Although both phrase-types lie between the same frequencies, a comparison shows that in the less frequently sung phrase (B), new notes have replaced the usual ones in the central part of the phrase, resulting in an increase in the length of the phrase. The end syllables remained the same, however. Male K showed a similar pattern in his two song-types.

In all males the length of the phrase was varied by adding or deleting the end syllable (Figures 9.10A and B). Other variations heard were singing part of a phrase and then stopping, and singing two phrases without the usual pause between them (e.g. male P, Figure 9.12H).

Song phrases of 15 males were reproduced as sonagrams (Figures 9.11 and 9.12). Eleven of the males had song phrases which had the same syllables arranged in the same sequence. (This includes the dominant phrase-type sung by male 118.) Some neighbouring males had very similar songs, even when neighbours changed between the two breeding seasons.

Figure 9.9

The two song-types of male 118 (recorded 28-12-77).

A) The commonest phrase

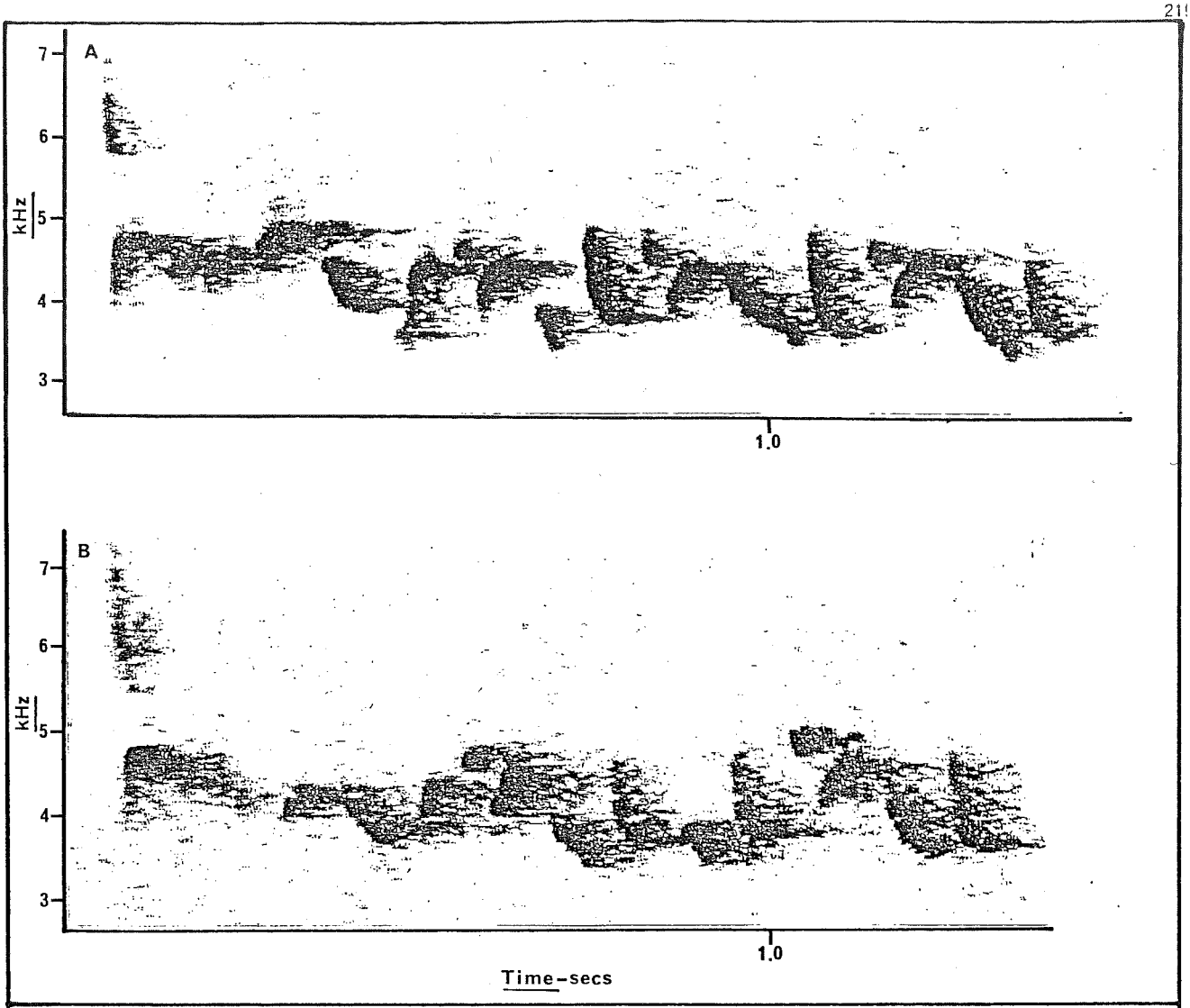
B) The less frequently sung phrase

Figure 9.10

Deletion of the end syllable (male 3, recorded 15-12-77).

A) Without the end syllable

B) With the end syllable added


A
B
kHz
7
6
5
4
3
1.0
Time-secs

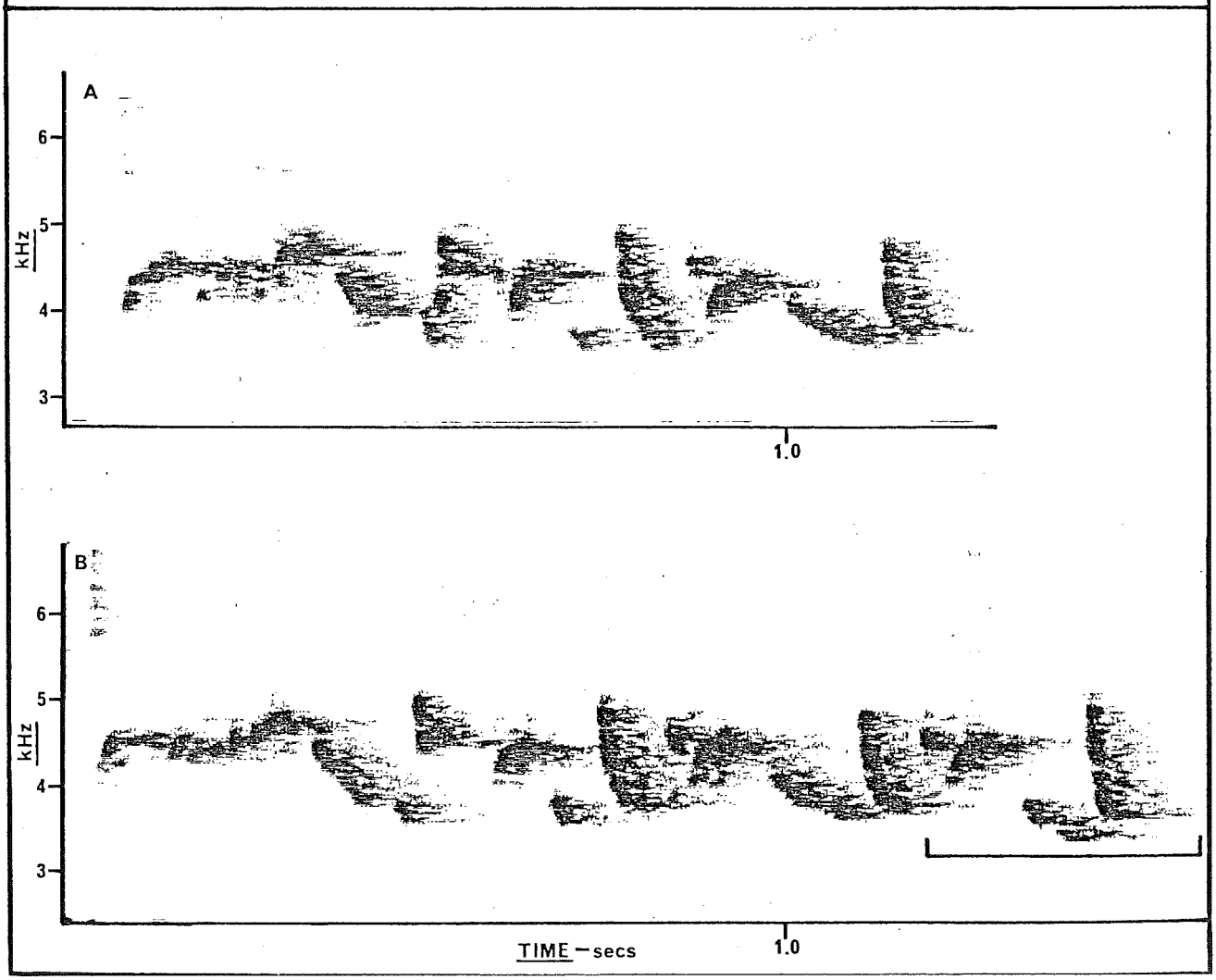

A
B
kHz
6
5
4
3
1.0
TIME – secs

Figure 9.11

Male song phrases: males recorded during the 1977 breeding and post-breeding seasons. Recording date in brackets.

A) Male 149 (18-3-78).

This male was resident along the top border of territory 5 (see Figure 4.3) for a short period, eventually disappearing. Note the similarity to the song of male 5.

B) Male 5 (= male 113) (8-1-78)

C) Male 3 (15-12-77)

D) Male 2 (= male 118) (28-12-77)

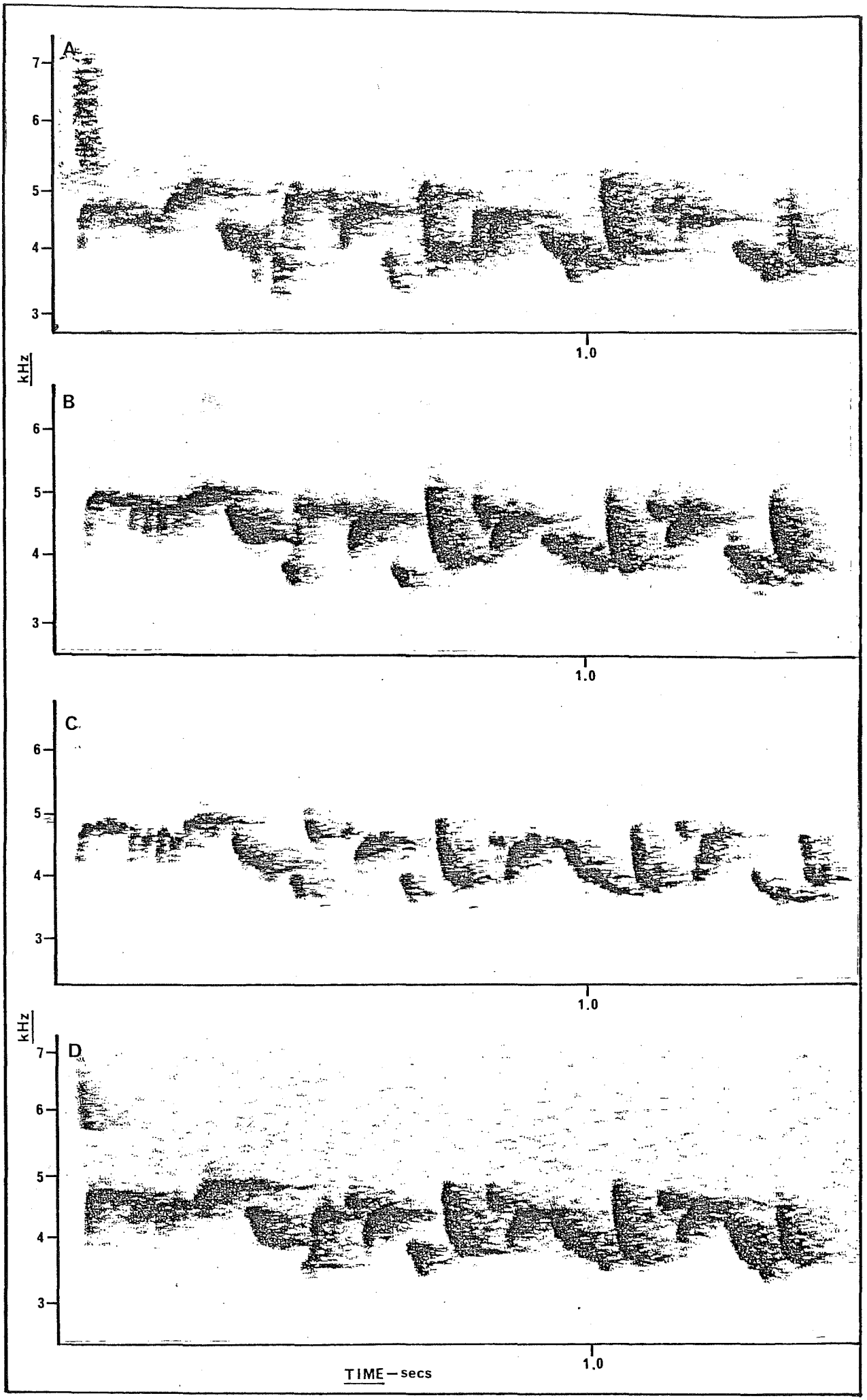

A
B
C
D
kHz
kHz
7
6
5
4
3
1.0
TIME — secs

Figure 9.12

Male song phrases: males recorded during the 1978 breeding and post-breeding seasons, or resident on territories after the 1977 breeding season. The sonagrams are arranged so that neighbours are together (as in Figure 4.6). Recording dates are given in brackets.

A) Shearing shed male (12-4-79).

This male was resident in the bush adjacent to the shearing shed by the main stream (see Figure 2.4) and had no neighbours.

B) Male A (14-9-78)

C) Male C (30-10-78)

D) Male D (= male 126) (8-11-78)

E) Male E (28-3-78)

F) Male G (30-9-78)

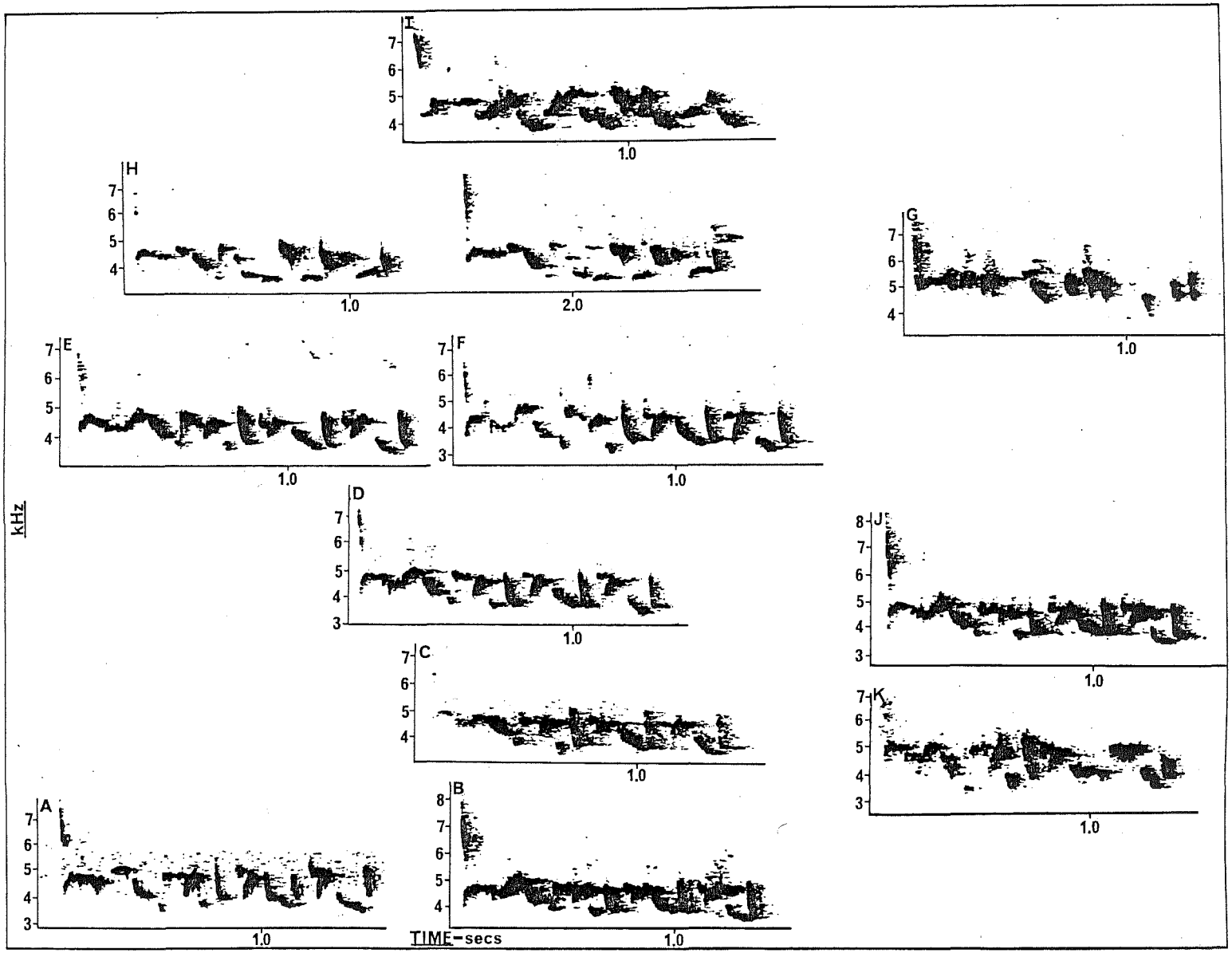
G) Male K (12-10-78)

H) Male P (20-11-78)

I) Male S (17-11-78)

J) Male 131 (25-3-78)

This male was originally resident in territory H, but disappeared during the following winter. His place was taken by male H (K).


I
H
G
E
F
D
J
C
K
A
B
kHz
TIME-secs
1.0
2.0

Given the slight variability in each male's song, the identification of these 11 birds from their song alone (except when male 118 sang his two phrase-types) was virtually impossible. As a result of this, complications arose when trying to determine if certain unbanded males were resident on one territory from one breeding season to the next This was the case for males 3 and G. I suspected that they may have been the same bird but could not confirm or deny it from a comparison of the sonagrams of their songs, due to their similarity to songs of other known birds.

Four of the males recorded, however, had very different song phrases (males 131, K, P, S). These males could be recognized immediately whenever they sang. The structure of the song phrases differed from the phrases of the 11 other males. They also differed from each other. The starting note to each phrase, however, was similar in all the males.

Males with similar songs still reacted to a tape of a song sounding like theirs, when it was played in their own territory. They also investigated a tape-recording of their own song.

The resemblance between the songs of some neighbouring birds was marked; but small, consistent differences did exist between them. These included the delivery rate of the phrases and the time interval between them, the timing of delivery of the syllables within the phrase and the emphasis placed on them, and the maximum, minimum and mean frequencies. Bisset (1978) found similar differences between songs of different Pied tits.

Therefore, within the study area a low variability in song-type was displayed. The number of neighbours a bird had, may have played a role in the type of song given. Where regular boundary patrolling occurred, males answered each other with similar songs, but in territories where the resident birds had few interactions with their

neighbours, their songs tended to be more individualistic.

9.4.5 Dialects

The similarity between the songs of the majority of the male tits within the study area suggested that a dialect may have evolved. This would be aided by the fact that Mount Fitzgerald Scenic Reserve is in an island situation (being surrounded by pasture) and that the tits remain in the same area all year round. Therefore, the population of tits in the Reserve is probably a self-perpetuating unit, receiving little or no immigration from nearby areas.

Although no recordings were made, subjective analysis suggested that the tits resident in Purau Track and Mount Sinclair Scenic Reserves (about 1 km from Mount Fitzgerald - see Figure 2.1) also had a dialect. Several males were heard singing phrases with a distinctive syllable placed in the middle of them. They sounded very different from those heard given by the Mount Fitzgerald population. It is a well-established fact that the singing patterns of isolated populations of a species often differ (Marler and Hamilton, 1966).

There may be a number of factors influencing the type of song a male tit sings. After the juvenile moult, the song of the male passed through a plastic stage, during which several different phrase-types were sung. Only later did song develop. It may be during the period of plasticity that the songs of neighbouring males influence the final form of the song sung by the immature male.

Male 131 had a song type differing from all the other males (Figure 9.12J). This male maintained a territory from early January onwards and was in juvenile plumage when he took up residence. He developed his song in isolation from other tits because he had no near neighbours. Therefore, genetic effects and the influence of neighbouring males may interact during this period of plasticity and ultimately

determine the type of song a male sings.

Male 126, resident in territory D, developed his song while males 2 and 3 were still present in the area. His song was very similar to the songs of these males (Figures 9.11 and 9.12). Therefore he may have learned his song from them. The importance of genetic effects could only be determined by raising birds in isolation.

A direct comparison can be made with the Splendid Sunbird *Nectarinia coccinigaster*, in West Africa. These birds formed dialects within an area of about 1 km . Sunbirds were resident on territories all year round, the males using a simple song for territorial advertisement. Neighbouring males had very similar songs with the main difference being in the presence or absence of the terminal note. A few males, however, had very different songs (Grimes, 1974; Payne, 1978). Payne suggested that the songs of neighbouring males were similar because they copied each other, i.e. social adaptation, whereas Grimes suggested that the young birds remain near the adult birds long enough to learn the home dialect. As a result, they were more likely to remain in that area and breed with birds having the same dialect than shift to another area with a different song type.

9.5 CONCLUDING COMMENTS

The catalogue of vocalizations presented and described in this chapter demonstrates the wide variety of calls and song used by the Yellow-breasted tit to convey different types of information. A similar variability in the repertoire of Pied tits (Bisset, 1978) and Chatham Island tits (Hay, 1975) has also been shown to exist.

Call notes were used, in the main, as contact calls between birds, and to impart information about territory defence, location of individuals, and alarming stimuli. Song functioned in territory

advertisement and defence, but did not appear to be an important factor in attracting a mate, as many birds were paired before the males had developed full song. Bachelor males, however, may have sung regularly in an attempt to attract an unattached female.

If the same recording of a song was played in the same part of a male's territory over several days, the resident male initially reacted aggressively towards it, but his response gradually weakened until he finally disregarded it. This demonstrated that males could recognize individual songs and may have accepted the taped song as a neighbouring male. Male tits also reacted aggressively towards tapes of songs of tits from other parts of New Zealand. (Songs used were of a Yellow-breasted tit from Eglinton Valley (from a record by Bigwood and Bigwood, 1976) and a Pied tit (from a record by McPherson, 1973).) Similarly, Yellow-breasted tits at Kaikoura reacted to tapes of males recorded at Mount Fitzgerald, by singing in reply and flying in to investigate. Therefore, male tits recognized the essential elements of these songs even though they were audibly different. Bisset (1978) obtained a similar result for Pied tits.

Duetting, in which members of a pair either sang more or less together, or antiphonally, as seen in the Snares Island fernbird (*Bowdleria punctata caudata*) (Best, 1973), did not occur in the Yellow-breasted tit. The only regular exchanges between members of a pair occurred when birds counterticked or countercalled.

CHAPTER 10

SPATIAL HETEROGENEITY AND THE DISTRIBUTION OF TITS

10.1 INTRODUCTION

Discontinuities in the environment produce an environmental patchwork which can be expressed in both vertical and horizontal dimensions, and can be present on any scale. Localized random disturbance, such as fire, erosion, or tree windfalls, may create patches of more immature successional status than their surroundings. If the patches differ in quality, for example in the resources they offer, then individuals should be expected to exhibit some degree of patch or habitat selection (Wiens, 1976).

For the two years of this study, the distribution of tits and territories in Mount Fitzgerald Scenic Reserve was non-random, in that tits restricted their activities to particular parts of the Reserve.

This chapter examines some of the factors which might influence the distribution of tits in this type of habitat.

10.2 POSSIBLE FACTORS INFLUENCING DISTRIBUTION

During the two breeding seasons monitored, a number of territory-holding birds relocated their territories elsewhere, or unaccountably disappeared. This occurred only in one part of the study area - along the main stream below the Reserve (see Figure 2.4), and involved three pairs of tits and one bachelor. These disappearances resulted in no adult tits inhabiting this area by the end of the breeding seasons.

Pair A, present along stream A (Figure 4.6) at the start of the 1978 breeding season, shifted its activities to a new territory further up

the stream (area A2, Figure 4.6), near the end of September 1978. The territory these birds abandoned was composed of a fringe of bush along the stream. No litter or shrub layer was present in this area. The area they shifted to was similar and it is not known if they bred successfully.

Two pairs disappeared from the same area during the two seasons. In the 1977 breeding season, territory 1 (Figure 4.2) supported a pair which fledged a brood and then moved with the fledglings away from that territory during early November, and eventually disappeared above territory 2. In all other known pairs, the female rebuilt within about three days of the previous brood fledging. However, this female continued to assist the male in feeding the chicks. This pair was not seen again. A new pair, located in the same territory (= territory C, Figure 4.6) in the 1978 season, disappeared at about the time the first brood should have fledged. They appeared to have abandoned the territory and were not seen again. Similarly, male B, a bachelor, also disappeared from his territory during the 1978 season.

These disappearances suggest that the habitat was, in some way, suboptimal. One of the limiting factors may have been food supply, as the resident birds (the males in particular) were commonly seen moving about on the bush edge searching for food. This can be contrasted with other territories on the bush edge in other parts of the study area, in which the resident birds were rarely seen in such areas. Territory sizes were also similar to those in other parts of the study area.

Suboptimal territories have been found to have an effect on the breeding success of other species. For example, Krebs (1971) found that Great tits (*Parus major*), breeding in suboptimal habitat, had a lower reproductive rate than birds in optimal territories in a more favoured vegetation type. These birds moved into more optimal habitat when the residents were experimentally removed from their territories.

There was no movement in the other direction when birds in suboptimal territories were removed.

Particular areas of the Reserve remained uninhabited by adult birds during the two breeding seasons. This was most evident in areas which did not contain running streams, for example in the area above the study area between the main stream and the east fence (Figure 2.4). All territory-holding adult birds had at least one continually running stream bordering on, or passing through, their territory. The terrain did not appear to influence the suitability of an area for residence.

Another possible factor affecting residency was the vegetation pattern within the Reserve. This can be related to the history of the area (see Chapter 2). The areas which had been most modified by man, through milling and burning, were the areas in which few tits were found, or they moved out of during the breeding season. The regeneration in these localities was very dense, with the shrub layer (when present) being almost impenetrable in places. This may have inhibited the movement and feeding behaviour of the tits.

Skinner (1978) noticed that the distribution of Pied tits in the Waitakere Range was influenced by vegetation type. Tits were not present on *Leptospermum* dominated land which had formerly been used for farming or gumdigging, and were only present in low numbers where *Leptospermum* and *Pinus radiata* merged on old gumdigging land. They were commonest in the least modified habitats, i.e. virgin bush. Gibb (1961) also found Pied tits had a patchy distribution in Kaingaroa State Forest. They were present in some types of exotic vegetation, but not in others. Foliage type and tree density may have played a determinant role. A similar situation existed for the Yellow-breasted tit in Ashley State Forest (pers. obs.), where birds were present in mature, open *Pinus radiata* with sparse undergrowth but absent in areas with a denser stocking rate and a more-closed canopy. At Kaikoura in Mount Fyffe

State Forest, tits were observed in rimu and podocarp dominated forest during the breeding season but not in bordering regenerating areas (pers. obs.). They were usually absent from Kowhai Bush at Kaikoura where the South Island robin breeds successfully. The South Island robin also shows a patchy distribution within its range (Flack, in prep., b).

During the end of the breeding season and in the post-breeding season, juvenile and immature tits were found in areas in which adult birds had not maintained territories. By the next breeding season, however, the majority of these birds had disappeared while those remaining were once again confined to those areas occupied in the previous breeding season.

The vegetation pattern may play an important role in determining such a distribution. *Fuchsia* dominated the canopy throughout much of the Reserve and, because it is deciduous, large areas had little leaf-cover over the winter. This may, in turn, effect prey abundance. As a result, those areas with less fuchsia and a wider variety of vegetation layers may be preferred habitats. Birds which cannot survive in less optimal areas may die or leave the area. The effect of the weather over the winter may also be important.

Therefore, only a small proportion of birds survived from one breeding season to the next. This explains why some territories had only one or two neighbours. As optimal areas appeared to be patchily distributed, only a few birds were able to maintain territories in such areas. More territories were present in the larger optimal patches, and regular boundary patrolling occurred along the shared borders. In small patches, where one or two territories were maintained, boundary patrolling and singing occurred less frequently.

The idea of optimal areas can be used to explain why birds which survived the winter on a territory later abandoned it during the breeding

season. Birds resident on such territories had been so, in some cases, since the end of the previous breeding season and were juveniles bred during that season. Over the winter, prey abundance may have been sufficient to maintain them, but insufficient when an increased food supply was necessary for breeding activities, i.e. these areas became suboptimal during the breeding season.

This habitat, therefore, may be supporting the maximum number of breeding pairs possible for the resources available. The presence of a few floaters at the start of the 1977 breeding season may indicate that all optimal habitats were occupied. One area not occupied during the 1977 season was territory H. A juvenile pair was resident in this area from early January 1978 onwards. They probably fledged one brood during the following breeding season. However, over the 1979 winter, the female (who was banded), and possibly the male, abandoned this territory and moved throughout territories A, B and C. Their place was taken by an unbanded pair of tits. This territory may have been bordering between optimal and suboptimal. (It is also an area recovering from recent disturbance.)

Factors influencing the distribution of tits, therefore, probably include the vegetation pattern (vertical and horizontal), species composition, food availability, and the weather over the winter. The suitability of the habitat may change over time with a change in the vegetation structure.

CONCLUDING COMMENTS

This study served as a general investigation of the biology of the Yellow-breasted tit, and could form the basis for more quantitative work on this and related species.

The importance of choosing a study area with accessible nests was highlighted during this study when only a few observations could be made on nest contents during the incubation and nestling stages. Further direct observation is needed to determine the exact delay before laying, the incubation period, and the physical development of the nestlings.

Other aspects which could be investigated in greater detail include:

1) The feeding biology, particularly whether any invertebrate prey types are taken in disproportionate numbers, i.e. is there selective feeding?
2) The function of the wing displays in apparently non-aggressive situations.
3) The extent of the movement by young tits away from their natal area, i.e. dispersal. This would necessitate the banding of nestlings. Banding studies would also reveal breeding site fidelity over a number of years.
4) The mechanisms producing the similarities between the songs of neighbouring males. Also, as males reacted to the songs of males from other populations, the elements of a song necessary for this recognition could be investigated.

SUMMARY

The biology of the Yellow-breasted tit (*Petroica macrocephala macrocephala*) was studied from an ecological and behavioural point of view in Mount Fitzgerald Scenic Reserve on Banks Peninsula. Detailed observations during 1977-1979 were made on about 130 tits, 33 of them being colour-banded.

1) THE STUDY AREA: The study area encompassed about 16 ha of mainly second-growth broadleaf bush dominated by *Fuchsia excorticata*. Remnant totaras (primarily *Podocarpus hallii*) were scattered throughout the area. Three types of habitat were recognized on the basis of the vegetation regeneration patterns resulting from the past history of the Reserve.

2) MIST NETTING RESULTS: By using mist nets, 16 male and 17 female tits were captured and colour-banded. A standard set of 14 measurements was taken from each bird after it had been placed in one of four classes as determined by its sex and plumage type. Males had statistically greater wing, tail and total lengths than females. Tits in juvenile plumage had smaller frontal spots than birds in adult plumage.

3) TERRITORIAL BIOLOGY AND THE MOVEMENTS OF TITS: Pairs of tits remained on a territory throughout the year. The areas of 20 territories found during the two breeding seasons varied between 0.49 and 2.57 ha. Only one territory was enlarged during the breeding season. Over winter, territories on the bush edge increased in size as the resident birds searched for food in the fields. A minimum territory size of about one hectare appeared to

be a prerequisite for successful breeding in this type of habitat.

Territorial activity was at a peak during the late prebreeding season and breeding season. Only the males were involved in territory maintenance activities. The commonest form of territorial advertising was song, often resulting in countersinging between neighbours along a shared boundary. Trespassing birds usually remained silent. If a dispute arose over territory, aggressive displays and postures were used. Fighting rarely occurred.

Some juvenile males and females moved away from adult territories in a synchronous movement, five to six weeks after independence and maintained territories in formerly vacant areas. Pair-bonds could be formed at this stage. Juveniles remaining on adult territories either set up subterritories on the peripheries of these territories or moved about continually. Juveniles occupying formerly vacant areas appeared to have a greater chance of surviving to the next breeding season than those remaining on or about adult territories.

4) NEST SITES AND NESTS: The female built cupular nests in four site-types in my study area: holes or cavities in trees; ledges or forks in trees; bush lawyer tangles or shrubs; and on the sides of trunks of tree ferns. The nest was of two parts - the base, the size of which varied from site to site and was constructed of coarse materials; and the cup, which was constructed of fine mosses and tree fern scales and lined with feathers.

Nests were built between 1.75 m and 8 m above the ground. Nest boxes were not used, probably because natural nest sites were not limiting.

5) THE BREEDING SEASON: All pairs began breeding activities in early September over about a 10-day period. Only the female built the

nest, which took no more than five days to complete. There was a delay of up to 11 days before the first egg was laid. For subsequent nests this delay dropped to between one and four days. Clutch size varied between three and five eggs, with four being usual. Circumstantial evidence suggested that a six egg clutch can be laid, as in a nest from which five chicks fledged, an egg was found pushed down into the nest lining. An average incubation period of 16 days was calculated, with the nestling period lasting about 18 days. Up to three broods were fledged in a season.

The male fed the female during building, laying and incubation, but not after the eggs had hatched. Nest attentiveness during incubation was about 72.5%. Rebuilding took place within 1-2 days of nest abandonment and 2-3 days after the chicks had fledged. If the female did not rebuild after the chicks had fledged, she assisted the male in feeding the fledglings. The dependent fledgling stage lasted about 19 days. Fledglings caught their own food regularly after about 15 days. The behaviour of tits of all ages during the breeding season is described.

The breeding cycle from laying to hatching took approximately 37 days, with the breeding season lasting up to 22 weeks for some pairs. This allowed a maximum of three broods to be raised.

6) PLUMAGE AND MOULT: Both sexes had distinctive juvenile and adult plumages but only females had a creamy white eye ring. Juvenile males sometimes had a few white feathers scattered about the black skin of their eye ring.

Moulting occurred once a year. Adults passed through a full moult once breeding activities had ceased. Juveniles went through a partial moult in which only the body feathers were replaced, 7-9 weeks after fledging. The juvenile moult lasted approximately 6-8 weeks whereas the adult moult took about 3 months.

The frontal spot developed fully during the juvenile moult in males, but in females it developed in the weeks following the completion of the moult.

7) FEEDING BIOLOGY: Tits foraged either in pairs or individually, but never with birds of other species. All levels of the vegetation profile were searched for prey, but tits were most commonly seen scanning the ground and lower understorey (0-4 m). They did not move about on the ground, however. All possible sites harbouring prey were examined.

A passive "watch and wait" strategy was used when searching for food. This involved the bird scanning the area in front of it from a vantage point. Two variations of this searching behaviour were employed and, when combined with the four ways of catching the prey, a wide variety of prey niches could be exploited. Foot trembling may have been associated with prey capture.

All types of invertebrate prey were taken, the birds apparently feeding opportunistically. Berries may have been eaten occasionally. Faecal sac analysis confirmed the identity of some prey-types eaten.

8) VOCALIZATIONS: Adult male song was the most distinctive of the wide variety of vocalizations used by Yellow-breasted tits of all ages. The calls given and their contexts are summarized. Sonagrams showed the structure of, and relationships between, some of the calls.

Call notes served as contact and locations calls, and included tick, simple, and nestling and dependent fledgling calls, and complex sounds. Developmental subsong developed into full song in males after passing through an unstructured stage, whereas non-developmental subsong was given by birds as they moved about

searching for food and was composed of a number of stereotyped complex notes.

The development of male song was followed through from the dependent fledgling stage. After passing through a plastic stage after the juvenile moult full song developed. It may have been learned from neighbouring males. Male song was stereotyped with the majority of males having only one song-type. Some neighbours had very similar songs. Because of its isolation, this population of tits may have developed a dialect.

9) SPATIAL HETEROGENEITY AND THE DISTRIBUTION OF TITS: The patchy distribution of tits within Mount Fitzgerald Scenic Reserve is possibly due to the presence of optimal and suboptimal patches of habitat. Possible factors influencing distribution and population density are vegetation patterns and species composition, food availability and the weather during winter. This habitat may be supporting the maximum number of breeding pairs possible.

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APPENDIX 1. Vegetation Structure of the Study Area

Emergent Species	Common name
Podocarpus hallii	Hall's totara
P. spicatus	Matai (Black Pine)
P. dacrydioides	Kahikatea (White Pine)
Hoheria angustifolia	Narrow-leaved lacebark
Pseudopanax crassifolium	Lancewood
Griselinia littoralis	Broadleaf (Kapuka)
Commoner Canopy Species	
Pseudowintera colorata	Pepper tree (Horopito)
Fuchsia excorticata	Tree fuchsia (Kotukutuku)
Pittosporum eugenioides	Lemonwood (Tarata)
P. tenuifolium	Black Matipo (Kohuhu)
Hoheria angustifolia	Narrow-leaved lacebark
Carpodetus serratus	Putaputaweta (Marble leaf)
Pennantia corymbosa	Kaikomako
Neopanax arboreum	Five-finger
Coprosma rotundifolia	—
C. linariifolia	Yellow wood
Cyathea smithii	Tree fern
Samburus nigra (Introduced)	Elderberry
Middle Storey Species	
Pseudowintera colorata	Pepper tree (Horopito)
Melicytus ramiflorus	Mahoe (Whitey wood)
Schefflera digatata	Pate
Coprosma rotundifolia	—
C. parviflora	—
Hebe salicifolia	—
Cyathea smithii	Tree fern
Ground layer (Ferns)	
Phymatodes diversifolium	Hound's Tooth
Asplenium spp.	—
Blechnum spp. (including *B. minus* and *B. discolor*)	—
Polystichum vestitum	—
P. richardii	Shield fern
Leptolepia novae-zealandiae	—
Vines	
Clematis paniculata	Clematis
Rubus cissoides	Bush lawyer
Rubus spp.	" "
Parsonsia sp.	—

APPENDIX 2. Measurements of Yellow-breasted tits.

	Ring No.	Capture date	Weight	Wing	Tail	Bill length	Bill width	Bill depth	Whiskers	Total length	Mid toe	Mid claw	Hind claw	Tarsus	Spot width	Spot depth	No. of recaptures
Males in adult plumage	106	1-9-77	11.0	75.0	49.8	9.8	4.3	3.2	-	-	13.6	7.0	7.6	24.6	7.0	2.8	0
	107	2-9-77	11.0	75.0	45.4	10.0	5.0	3.1	-	-	13.8	4.8	6.3	24.7	7.1	2.4	0
	108	11-9-77	11.0	73.0	51.8	10.8	4.8	3.4	-	-	14.9	5.3	6.2	25.2	6.1	1.7	0
	113	12-9-77	11.0	68.0	50.4	10.4	4.8	3.1	9.0*	-	12.2	5.2	6.2	25.0	6.6	2.2	1
	118	24-9-77	12.0	72.0	52.9	10.7	4.2	3.4	-	-	12.7	5.0	5.9	22.8	7.6	2.8	0
	149	10-3-78	10.0	72.0	50.2	10.8	3.9	3.4	10.0	-	13.4	5.6	6.3	25.8	5.4	3.0	1
	203	6-4-78	12.0	78.0	51.0	9.7	4.0	3.0	10.8	121	11.9	4.9	6.8	27.2	7.0	3.6	0
	209	11-4-78	12.0	74.0	48.2	10.0	4.3	3.4	10.9	118	11.5	5.2	6.8	27.0	6.5	2.1	0
Females in adult plumage	102	23-6-77	12.0	68.0	40.4	8.7	3.6	3.2	-	-	15.4	5.4	7.2	23.6	6.2	1.7	0
	200	7-7-77	10.5	73.0	51.8	9.6	4.4	3.1	-	-	12.0	5.6	8.0	26.0	6.6	1.7	0
	109	11-9-77	11.0	70.0	49.7	10.2	4.6	3.1	-	-	13.2	4.8	6.3	24.5	6.2	2.0	0
	111	11-9-77	11.0	71.0	49.5	11.0	4.4	3.0	8.5*	118*	12.7	4.7	6.4	23.7	5.2	1.2	3
	161	18-3-78	11.0	67.0	42.3	10.0	4.0	3.0	8.8	112	12.5	5.5	5.9	24.8	6.6	2.0	0
	207	11-4-78	10.5	70.0	45.0	9.2	4.0	3.1	9.4	114	10.5	4.8	6.5	26.9	5.5	0.8	0
	208	11-4-78	11.5	74.0	54.1	9.6	3.9	3.2	9.5	124	12.1	5.2	6.8	27.6	7.5	2.0	0
	210	27-4-78	11.0	72.0	48.0	10.1	4.0	3.4	9.4	114	12.4	5.0	6.0	25.6	6.8	1.2	0
	212	6-5-78	11.0	74.0	45.1	10.3	3.9	3.2	10.2	111	-	-	-	-	-	-	0
	214	8-5-78	10.5	71.0	45.6	9.8	3.9	3.1	9.8	113	12.8	4.9	6.2	24.8	5.8	1.5	0
	236	9-3-79	12.5	70.0	45.0	9.0	4.0	3.9	9.2	116	12.5	5.5	6.8	24.9	6.3	1.4	0
	248	13-5-79	11.0	74.0	43.8	9.6	4.2	3.1	8.5	118	12.2	4.9	7.9	25.2	6.0	1.5	0
Males in juvenile plumage	125	29-1-78	14.0	75.0	51.3	10.2	4.3	3.2	7.3	-	12.1	5.7	7.2	24.8	5.0	2.2	0
	126	29-1-78	10.0	75.0	49.2	9.3	4.2	3.6	11.0*	116*	13.8	5.2	6.6	24.6	4.8	1.2	1
	128	30-1-78	9.0	74.0	49.4	10.0	4.2	3.1	7.7*	-	11.0	5.6	7.2	24.8	5.2	0.8	1
	131	30-1-78	10.0	73.0	51.0	9.4	4.1	3.1	10.6	-	13.4	5.6	6.5	25.0	4.9	2.0	0
	159	16-3-78	13.0	74.0	49.0	10.2	4.5	3.5	8.9	120	11.4	5.2	6.5	28.6	5.8	3.4	0
	W/G/W	8-2-79	13.0	75.0	53.0	9.1	4.6	3.6	9.5	118	13.6	6.0	7.0	24.0	5.6	0.5	0
	234	9-3-79	14.5	75.0	51.3	9.3	4.4	3.6	9.3	122	14.9	5.0	6.2	24.3	5.8	2.0	0
Females in juvenile plumage	133	30-1-78	11.0	71.0	47.7	9.6	4.5	2.9	10.5	-	13.2	5.2	5.6	26.0	Only faintly present		0
	140	15-2-78	12.0	68.0	43.4	10.4	4.8	3.2	8.8	-	11.2	5.0	6.5	24.1	5.0	1.4	0
	141	15-2-78	12.0	69.0	43.2	11.4	4.5	3.2	8.1	121*	11.2	5.0	6.2	24.8	5.4	1.1	1
	152	14-3-78	12.0	69.0	48.6	10.9	4.0	3.0	11.1	114	10.8	5.2	6.3	27.0	5.1	1.0	0
	W/G/W	11-2-79	12.0	72.0	46.5	9.0	4.7	3.2	9.2	116	12.8	5.4	6.2	24.0	5.9	0.4	0
18 day old male	123	2-11-77	-	56.0	25.0	9.2	5.0	3.0	-	-	13.7	4.2	6.1	25.6	Only faintly present		0

— not measured

* from recapture data

Weight in grams. All other measurements in millimetres.

APPENDIX 3. Summary of variables measured for other species.

Species			Weight	Wing	Tail	Bill length	Bill width	Bill depth	Whiskers	Total length	Middle toe	Middle claw	Hind claw	Tarsus
Grey Warbler		$\bar{X}$	7.02±0.19	54.65±0.38	43.55±0.42	8.42±0.14	3.44±0.06	2.47±0.04	5.85±0.16	108.5±1.02	8.22±0.21	3.88±0.06	4.39±0.07	22.35±0.26
		n	19	20	19	20	20	20	18	18	17	20	19	15
		R	6.0 - 8.5	50.0 - 57.0	40.7 - 47.1	8.1 - 10.0	3.0 - 4.0	2.2 - 2.8	4.4 - 6.8	101 - 115	6.7 - 10.0	3.4 - 4.2	3.8 - 4.9	20.5 - 24.0
Fantail		$\bar{X}$	9.0±0.62	72.25±1.50	85.30±1.33	7.89±0.20	4.25±0.17	2.82±0.07	11.0	151	9.02±0.28	4.28±0.11	5.83±0.17	23.92±0.33
		n	7	8	8	8	8	8	1	1	8	7	7	7
		R	6.0 - 10.0	64.0 - 76.0	80.0 - 91.0	6.9 - 8.7	3.9 - 5.2	2.5 - 3.1	-	-	7.9 - 9.7	3.9 - 4.6	5.2 - 6.4	22.2 - 25.1
Redpoll		$\bar{X}$	11.50±0.31	67.90±0.50	48.57±0.58	8.76±0.22	5.02±0.07	6.00±0.07		114.6±0.90	8.11±0.15	5.10±0.18	6.50±0.24	16.20±0.12
		n	21	21	21	20	20	20	-	9	18	20	20	18
		R	9.0 - 14.0	64.0 - 72.0	43.9 - 54.0	7.4 - 10.6	4.4 - 5.7	5.4 - 6.8		111 - 119	7.1 - 9.1	3.5 - 6.2	4.9 - 8.2	15.2 - 17.0
Brown Creeper		$\bar{X}$	12.78±0.38	58.42±0.43	51.00±0.96	8.84±0.16	4.16±0.09	3.78±0.09	6.52±0.24	116.8±1.13	10.91±0.31	4.83±0.10	6.06±0.15	26.02±0.35
		n	14	14	14	14	14	14	14	13	13	14	14	14
		R	11.0 - 14.5	56.0 - 61.0	47.0 - 59.0	8.0 - 9.9	3.8 - 4.9	3.2 - 4.5	4.8 - 7.8	110 - 121	9.3 - 12.6	4.0 - 5.2	5.1 - 6.9	24.3 - 28.3
Silvereye		$\bar{X}$	12.71±0.18	62.43±0.23	44.02±0.30	10.15±0.09	4.28±0.03	3.78±0.03		118.5±0.53	9.72±0.09	4.43±0.04	5.37±0.05	21.49±0.17
		n	69	72	66	68	70	69	-	52	62	69	69	69
		R	9.0 - 15.0	58.0 - 66.0	38.8 - 48.8	8.9 - 11.8	3.8 - 4.8	3.2 - 4.4		106 - 128	8.0 - 11.1	3.6 - 5.4	3.5 - 6.3	17.9 - 23.9
Goldfinch *Carduelis carduelis*		$\bar{X}$	12.66±0.29	76.0±0.95	44.28±1.69	11.84±0.17	5.68±0.14	6.88±0.13			12.10±0.19	5.70±0.26	6.90±0.28	17.10±0.32
		n	3	5	5	5	5	5	-	-	5	5	5	5
		R	12.0 - 13.0	73.0 - 78.0	40.4 - 49.2	11.2 - 12.1	5.3 - 6.1	6.4 - 7.1			11.6 - 12.7	5.1 - 6.6	5.8 - 7.3	15.9 - 17.8
Hedgesparrow *Prunella modularis*		$\bar{X}$	19.8±0.73	66.90±0.75	59.65±1.22	11.23±0.52	5.66±0.13	4.15±0.11		137.6±2.04	14.07±0.28	5.14±0.15	6.70±0.13	22.98±0.26
		n	10	10	9	9	8	9	-	5	8	9	9	7
		R	17.0 - 24.0	63.0 - 69.0	54.8 - 65.5	9.0 - 13.9	5.1 - 6.1	3.6 - 4.6		134 - 145	13.2 - 15.2	4.2 - 5.7	6.0 - 7.5	21.8 - 23.8
Chaffinch *Fringilla coelebs*	Male	$\bar{X}$	22.09±0.18	86.81±0.50	61.47±0.84	12.22±0.20	6.54±0.08	7.18±0.04		151	13.01±0.32	5.28±0.19	6.37±0.16	20.94±0.23
		n	11	11	11	11	11	11	-	1	10	11	11	11
		R	18.0 - 25.0	85.0 - 90.0	56.0 - 65.0	11.0 - 13.0	6.1 - 6.9	7.0 - 7.4		-	11.0 - 14.2	4.3 - 6.5	5.8 - 7.4	19.6 - 21.9
	Female	$\bar{X}$	21.25±1.18	77.60±1.21	52.50±1.33	12.10±0.26	6.80±0.43	6.72±0.30	4.7	145	11.86±0.30	5.58±0.36	5.93±0.40	20.75±1.02
		n	4	5	5	5	5	5	1	1	5	5	3	4
		R	18.0 - 23.0	73.0 - 80.0	48.0 - 55.8	11.4 - 12.7	6.0 - 8.4	5.6 - 7.3	-	-	10.4 - 12.7	4.9 - 6.8	5.2 - 6.6	18.0 - 22.8
Bellbird	Male	$\bar{X}$	31.5±1.18	88.67±0.78	77.89±1.33	14.98±0.28	5.18±0.04	4.57±0.08		183.0±6.24	14.19±0.42	6.72±0.26	9.58±0.29	31.13±0.65
		n	8	9	8	9	9	7	-	3	9	9	9	9
		R	28.0 - 36.0	86.0 - 93.0	72.7 - 83.3	14.0 - 16.3	5.0 - 5.4	4.3 - 4.8		174 - 195	12.1 - 15.7	5.8 - 8.1	8.2 - 10.8	29.2 - 35.9
	Female	$\bar{X}$	26.16±0.79	80.0±0.43	62.27±1.00	13.86±0.18	5.24±0.08	4.32±0.06		159.3±3.08	13.15±0.23	6.12±0.14	8.64±0.23	29.67±0.51
		n	15	16	16	16	16	16	-	9	13	14	14	15
		R	23.0 - 34.0	76.0 - 82.0	55.0 - 68.6	12.8 - 15.0	4.8 - 6.0	4.0 - 4.8		148 - 171	11.1 - 14.3	5.5 - 7.3	7.2 - 10.2	26.2 - 33.0
Greenfinch *Carduelis chloris*		$\bar{X}$	27.0	84.0	44.5	13.0	8.3	9.5		135	11.6	6.9	6.4	20.9
		n	1	1	1	1	1	1	-	1	1	1	1	1
		R	-	-	-	-	-	-		-	-	-	-	-

$\bar{X}$ = mean ± standard error

n = sample size

R = range.

Weight in grams.
All other measurements in millimetres.